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ACTUAL AND POTENTIAL YIELDS IN PHOTOSYNTHESIS[1]

by

DR. G. E. FOGG

THE ENERGY reaching the surface of the earth as radiation from the sun amounts to 5×10^{23} calories per annum. It will help you to appreciate the magnitude of this if I say that 2,000,000,000 nuclear power stations—about one for each man, woman and child on earth—would be needed to provide energy at an equivalent rate. Photosynthesis, the process in which radiant energy is converted by green plants into the potential chemical energy of organic substances usable as food or fuel, is at present the most effective means that we have of making use of this, our greatest source of power. Clearly, it is a matter of interest to estimate the yield of photosynthesis under natural conditions and to consider how this might be increased.

An estimate of the total yield of photosynthesis on the earth as a whole may be made by determining the productivities of different types of plant communities—forest, grasslands, desert, cultivated lands and the plankton of the sea—and summating these according to the area covered by each type. Adequate data for carrying out this deceptively simple task do not yet exist. Perhaps the most important attempt at such an estimate was made about forty years ago by Schroeder (1919). Using agricultural returns as his primary data he calculated the total annual yield of dry matter in various crop plants and on the basis of his results arrived at values for the average productivities of forests, steppe and desert by intelligent guessing. His final estimate was that the total net photosynthesis (i.e. photosynthesis over and above that required to compensate for the respiration of the plants) of land plants amounts to $1{\cdot}63 \times 10^{10}$ tons of carbon per annum. Subsequent workers have accepted Schroeder's results with little modification and I do not propose to attempt a completely new assessment here. However, while his estimate of the productivity of farmland is probably reasonably correct and while we are not yet in a position to question his figures for steppe or desert, there are grounds for thinking that he underestimated the yield of forest, which is the type of vegetation contributing most to the total ($1{\cdot}1 \times 10^{10}$ tons of carbon per annum).

Schroeder, on the basis of determinations on Bavarian forests, took 2,500 kg carbon/hectare/year as the most probable mean value for all types of natural forest. Recent determinations by Ovington and Pearsall (1956) give 1,700 and 3,200 kg carbon/hectare/year as mean values for the above-ground production, by deciduous and coniferous forest respectively, on soils below average agriculturally in Britain. To allow for roots and fallen leaves these values should be increased to at least 2,550 and 4,800 kg carbon/hectare/year to give total net production by photosynthesis. In extrapolating further to obtain a mean value for all forest land an indication obtained by Pearsall and Newbould (1957) that production is proportional to length of growing season (taken as number of days with mean temperature greater than 5°C) is useful. On this basis Schroeder's figure of 2,500 kg carbon/hectare/year does not seem an unreasonable one to take for both deciduous and coniferous forest, since Ovington and Pearsall's results were obtained in localities having a representative growing period for the former and one of about twice the average length for the latter. However, the most important unknown is

[1] Address delivered to Section K (Botany) on September 10, 1957, at the Dublin Meeting of the British Association. Dr. Fogg is on the staff of the Department of Botany, University College, London.

the production of tropical evergreen forest. Under this head we must put about half of the forest resources of the world and, apart from a strong impression that here we have plant life in its most vigorous state, we have no direct means of estimating its productivity. Accepting a production of 4,800 kg carbon/hectare/year as the mean value for evergreen forest with a growing season of 250 days, we might expect tropical forest to fix at least 7,000 kg carbon/hectare/year. This seems a reasonable value since it represents about 1 per cent efficiency in utilisation of the available light in tropical latitudes and various direct determinations have shown the photosynthetic efficiency of field crops and forests to be of this order under summer conditions (Rabinowitch, 1951). That it is unlikely to be an under-estimate is indicated by reports that a tropical crop, sugar-cane, is capable of fixing about 28,000 kg carbon/hectare/year. Finally, there are considerable areas of submarginal or exploited forest which, at a guess, may have an average productivity of 1,000 kg. carbon/hectare/year. An estimate of the net production of the world's forests is thus as follows:

	Mean production (kg C/hectare/yr.)	*Total area* ($km^2 \times 10^6$)	*Total production* (*metric tons* $\times 10^{10}$)
Coniferous forest	2,500	10·0	0·25
Deciduous forest	2,500	4·9	0·12
Tropical forest	7,000	14·7	1·03
Submarginal forest	1,000	14·0	0·14
Totals		43·6	1·54

With the values considered most probable by Schroeder for farm land, steppe and desert (0·43, 0·11 and 0·02 tons of carbon per annum respectively), the probable total net annual production by land plants is then $2 \cdot 1 \times 10^{10}$ metric tons of carbon. With a 15 per cent addition to allow for respiration by plants themselves this gives the gross production as $2 \cdot 4 \times 10^{10}$ metric tons of carbon per annum.

Schroeder at first considered that photosynthesis by plankton in the oceans is negligible but later conceded that it may be as much as double that of land plants alone. Because of the special problems involved in determining photosynthesis in natural waters we are still in much uncertainty about the order of magnitude of the contribution which plankton makes to the productivity of the earth. Whereas an approximate idea of the yield of photosynthesis by terrestrial plants is given by the dry weight of the crop produced on unit area in the course of one growing season, the magnitude of the standing crop of phytoplankton gives little idea of its productivity. Because the growth rate of phytoplankton is high and because there may be equally rapid loss through sedimentation and through grazing by plankton animals, the rate of turnover in the phytoplankton is high and direct determinations of rate of photosynthesis are necessary. Photosynthesis is determined, either from oxygen production or from assimilation of radiocarbon supplied as bicarbonate, in water samples suspended at different depths and the results are integrated to give the total carbon fixed per unit area of water surface. The radiocarbon method was used by Steemann Nielsen (1957) in an extensive series of productivity determinations during the world cruise of the *Galathea*. His results varied between 0·05 and 3·0 g carbon/metre^2/day; highest yields, corresponding to 6,000 kg carbon/hectare/year—about the yield of tropical rain forest—being found in the Benguela current off S.W. Africa. By far the largest parts of the tropical and subtropical regions of the oceans have a low productivity of between 0·1 and 0·2 g carbon/metre^2/day and on this basis Steeman Nielson put the average daily gross production in all seas as about 0·15 g carbon/metre^2/day, which is equivalent to 550 kg/hectare/year. Subsequent determinations in temperate and subarctic waters show rather higher productivities, e.g. an average value for the North Sea is 800 kg carbon/hectare/

year (Steele, in the press). Using as a basis a recent compilation of all available data made by by the F.A.O. (Fisheries Biology Branch), I estimate the annual production for the whole hydrosphere, the area of which is about three times that of the land, as $3{\cdot}2\times10^{10}$ metric tons carbon/year, rather more than that of land plants. This is considerably less than an earlier estimate made by Riley (1944) of $14{\cdot}6\times10^{10}$ tons, based on an average production of about 1 g carbon/metre^2/day indicated by oxygen measurements. Although the oxygen and radiocarbon methods agree well at moderately high rates of photosynthesis there is considerable divergence at low rates and it is not yet agreed which more nearly represents the actual rate. The main difficulty is that it is not yet clear whether the radiocarbon method determines net or gross production. If products of photosynthesis in which the radiocarbon is incorporated are respired preferentially then the final radioactivity of the plankton is a measure of net photosynthesis. If, however, products of photosynthesis are respired equally with other substrates for respiration then the method is more a measure of gross production. The difference between the two, slight where moderate rates of photosynthesis are concerned, becomes enormously important in the vast ocean deserts in which photosynthesis scarcely counterbalances the respiration of the bacterial flora which soon develops when a water sample is enclosed in a bottle. A further source of uncertainty is that the radiocarbon method only measures carbon fixed in the cells of the plankton organisms. It is known that soluble products of photosynthesis can escape from algal cells, but it is not known to what extent this occurs in the oceanic phytoplankton. It is clear that the plant physiologist can play an important role here in interpreting the results of the radiocarbon method to the oceanographer. At present we can only say that the estimate of $3{\cdot}2\times10^{10}$ represents a fairly firm lower limit and that the actual gross yield of photosynthesis in the oceans may well be greater than this, perhaps by a factor of 5.

We can therefore say that the total gross photosynthetic yield of the earth is at least $5{\cdot}6\times10^{10}$ metric tons of carbon fixed per annum. Rabinowitch (1945) has rightly emphasised the immensity of the process by comparing it with the total output of the world's chemical, metallurgical and mining industries, which is of the order of 10^9 tons annually. Nevertheless, the photosynthetic efficiency of the earth as a whole is very low, only about 0·2 per cent of radiation of suitable wave lengths being used. In short-term laboratory experiments green plants have been shown to be capable of at least 25 per cent efficiency in the conversion of the energy of visible light into potential chemical energy. Even the most prolific natural vegetation falls far short of this. The plankton of the Benguela current is less than 1 per cent efficient and sugar-cane, which seems to be the most efficient crop photosynthetically yet known, achieves a mean efficiency over the year of only 1·43 per cent.

Having given you some idea of the actual yields of photosynthesis under natural conditions I now want to discuss the possibilities of obtaining higher yields. I do not propose to discuss increases in total photosynthesis obtainable by extension of the areas occupied by productive vegetation; such increases are mainly dependent on the manipulation of factors affecting photosynthesis indirectly and their consideration falls in the province of the agriculturalist and pisciculturist. What I propose to consider briefly are increases in yields above those normally obtainable under natural conditions which might be brought about on an economic scale by application of our knowledge of the physiology of photosynthesis. Improvements of this sort are clearly desirable in densely populated countries in which maximum use must be made of agricultural land. I shall consider only total yields in dry matter without regard to the quality of the product. Here, I share the view of Pirie (1957) that it might be a good plan to reverse the normal procedure of husbandry and, instead of deciding what products are needed and then growing

the appropriate crop, to select a plant which gives a high yield under the local conditions and then to find uses for the material which it synthesises. With the further development of biochemical engineering this approach should become possible. Pirie, for example, has shown how high quality protein can be extracted from leaves on an economic scale.

A principal difficulty in the way of making best use of sunlight in photosynthesis is that the intensity is too high. Only at low intensities can light be used with efficiencies as high as 25 per cent, at high intensities the yield per quantum falls off progressively. This happens because the so-called dark reactions of photosynthesis become rate-limiting before the photochemical reaction. Thus, while for the engineer the difficulty in making use of sunlight is that its energy has to be concentrated, in making more efficient use of green plants the difficulty is that it is too concentrated. With land plants the only prospect of meeting this difficulty seems to be the partial one of selecting species for which saturating intensities for photosynthesis are high. Although the efficiencies at low intensities of all green plants appears to be the same different species vary considerably in their performance at high intensities. Furthermore, a given species of plant is not constant in photosynthetic properties but varies both in yield per quantum and in maximum possible rate of photosynthesis as it ages. This has been shown both for higher plants and algae. Thus it would be best to arrange things on a continuous basis, i.e. to have as a crop plant one which has a complete ground cover all the time and produces leaves continuously throughout the growing season and from which the product could be harvested continuously in the form of leaves which had passed their photosynthetic prime (Pearsall, 1954). It should not be impossible to find such a plant. A grass lawn approximates to this kind of system, although the light-absorbing capacity of grassland is poor compared with woodland; properly pampered a lawn would give high photosynthetic yields but I do not know of any measurements which have been made to show this. Our present crop plants are most unsatisfactory from this point of view; for most of the growing season they cover only a fraction of the ground and thus fail to absorb much of the available light and their maximum photosynthetic activity and maximum leaf area are only maintained for short periods and may not even coincide so that their period of intense photosynthesis may only last for a week or so (Watson, 1956).

Besides water, the concentration of which is not normally directly limiting for photosynthesis, the raw material for photosynthesis is carbon dioxide. The concentration of this in air, 0·03 per cent, is limiting for photosynthesis in bright sunlight and it has been shown in many experiments that crop yields can be increased from 50 to 100 per cent by increasing its concentration in the surrounding air tenfold or so. This is feasible in greenhouses and might be possible in open fields. Flue gases from adjacent industry would provide the cheapest source of carbon dioxide but care would be needed in removing toxic gases.

In many respects it seems easier to obtain high photosynthetic yields by using algae rather than higher plants. The difficulties in the way of increasing production of phytoplankton in the oceans and of harvesting the product are great. However, the possibility of growing mass cultures of algae has excited a great deal of attention recently (Burlew, 1953; Tamiya, 1957) and I should like to devote the space remaining to me to consideration of this.

A great attraction in using microscopic algae in this way is that it would allow a degree of standardisation in technique and product greatly superior to that attained in conventional agriculture and which would make for correspondingly greater industrial efficiency. Experimental work has so far been carried out almost entirely with species of *Chlorella* and *Scenedesmus*, but some research has been devoted to finding the best forms for mass culture. There do not appear to be any species which surpass *Chlorella* and *Scenedesmus* species in ease of culture and robustness.

Strains have been found which are resistant to high temperatures—a great advantage in culture exposed to the sun—and it has been shown that higher efficiencies can be achieved by using a strain appropriate to the prevailing conditions (Tamiya, 1957). *Anacystis nidulans*, a thermophilic blue-green alga which has been discovered in the course of the search for new strains, is the fastest-growing photosynthetic organism yet known, having a mean generation time at 40°C of about 2 hours (Kratz and Myers, 1955).

In dense cultures of algae, increase becomes proportional to the area of illumination and so mass cultures must be arranged to have high surface/volume ratios. The difficulty of making efficient use of full sunlight is greater with algae than with higher plants as algae generally have the character of 'shade' plants, rather than 'sun' plants, and are saturated at lower intensities. However, there is the possibility of making use of the effect of intermittent illumination to secure higher yields with algae. Briefly, if plants are given light in bright flashes, the 'dark' reactions of photosynthesis are able to 'catch up' in the intervening dark periods and thus enable a higher yield to be obtained for a given amount of light. In a sufficiently turbulent and dense algal culture, cells can be exposed at the surface for a brief interval and then be carried into darkness in the bulk of the culture. It is possible to achieve in culture the rather critical conditions needed for the intermittent light effect and yields have been increased by Davis, of the Carnegie Institution of Washington (Burlew, 1953), from 20 g carbon/metre^2/day in slowly stirred cultures to 34 g carbon/metre^2/day (equivalent to 124,000 kg carbon/hectare/year and representing about 7 per cent utilisation of solar energy) in cultures stirred with a rotor turning at 475 r.p.m.

The variations in photosynthetic efficiency of algae with age can be overcome comparatively simply by continuous harvesting, combined with regulated addition of fresh medium to keep the cell density at some suitable level. In this way the cells can be maintained at or near maximum photosynthetic efficiency. Provided that suitable temperatures are maintained it is also possible to have a fully effective light-absorbing surface throughout the year.

Carbon dioxide can be readily maintained at optimum level in algal cultures by aerating the medium with a suitable gas mixture and ensuring that the culture is kept in a state of turbulence sufficient to prevent diffusion gradients from being set up around the cells. As with higher plants the carbon dioxide could come from flue gases, but another way which seems to hold great promise is that the carbon dioxide should be generated within the culture itself by the bacterial decomposition of waste organic matter. This is what is done in the photosynthetic method of sewage disposal which is now being developed in California, New Zealand, and other places. Under suitable conditions *Chlorella* and certain other algae thrive in sewage, the oxygen which they produce accelerating the bacterial oxidation of the organic matter so that very effective stabilisation of the sewage is achieved. It appears that under these conditions growth of the algae is entirely dependent on photosynthesis and that there is little direct assimilation of organic substances by the algae.

Trials of large-scale algal cultures have now been carried out in several countries and results are summarised as follows:

					Net yield (g C/m^2/day)
Björkman *et al.*	1955	Outdoor tanks	Sweden	October	5
van Oorschot	1955	,,	Holland	June	5
Morimura *et al.*	1955	,,	Japan	August	11
Oswald & Gotass	1955	Sewage tanks	California	July	17
Mayer *et al.*	1956	Outdoor tanks	Israel	May	8·5
Thacker & Babcock	1957	Aseptic cultures Artificial light	New York	–	5·8

The largest scale culture so far attempted is a Japanese one of 78 metre^2 illuminated surface. It would not be legitimate to extrapolate from these results except perhaps in the case of those of Oswald and Gotass, from which one can say that yields of 3 to 4,000 kg carbon/hectare/year might be expected in sewage oxidation ponds. Bearing in mind that algae such as *Chlorella* contain a minimal proportion of inedible structural materials this is a substantial improvement on the yields of conventional crops.

Estimates have been made of the probable cost of *Chlorella* grown in culture. Thacker and Babcock (1957), who based their estimates on experiments conducted under rather carefully controlled conditions, estimated that under the most favourable conditions it would be about 50 cents/lb. Tamiya (1957) estimated the cost of *Chlorella* grown in open tanks under Japanese conditions to be 26 cents/lb. These prices are high compared with that of a comparable product such as ground soy beans, which cost 6 cents/lb., and it must be concluded that unless some radical simplification in technique or some particularly valuable algal product is found the process is unlikely to be economically possible in the near future. The cost of *Chlorella* from sewage oxidation ponds would, of course, be considerably less and it appears that it is only the lack of a cheap means of harvesting the alga which is preventing the economic development of this method. At present harvesting by high-speed centrifuge is the only practical method, and with the rather low algal concentrations which can be achieved this is expensive. Filamentous algae would be more easily harvested than *Chlorella*, but these have disadvantages from other points of view.

Perhaps the most serious obstacle to an increased use of solar energy by means of photosynthesis is that, from its very nature, the process cannot be carried out in the highly centralised manner which succeeds best under present economic conditions. Bearing in mind that in solar energy we have a virtually unlimited source of power and that its utilisation involves none of the hazards associated with nuclear fission, it seems well worth while devoting more effort to the overcoming of such obstacles.

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THE BIOCHEMISTRY OF YEAST FERMENTATION[1]

by

DR. R. DAVIES

I FEEL that I cannot start this paper without a brief reference to that famous French microbiologist Louis Pasteur, since it is just 100 years last month since he published his first paper on alcoholic fermentation. In that paper he said that fermentation was 'life without air, and conversely life without air resulted in fermentation'. He firmly believed that fermentation could not be divorced from cell growth and multiplication. We know now that he was wrong in that belief, but his definition of fermentation as life without air still stands. Pasteur believed that oxygen was necessary for life, but that in fermentation the oxygen could be abstracted from the sugars on which the organism lived. This view was strongly contested by Berthelot who suggested that it was the energy released during the breakdown of the sugar which was important for life and not oxygen *per se*. This energy resulted from reactions in which part of the sugar molecule was oxidised at the expense of the remainder, which was reduced. Berthelot's views are essentially those which we hold today, but at the time they were expressed they were swept aside by Pasteur.

The essence of fermentation is that by a series of internal oxidations and reductions energy is released from the substrate and is trapped in a form in which the organism can use it for synthesis of cell material. The principal compound which serves as a storehouse for energy in living cells is adenosine triphosphate, or ATP for short, which is a compound of adenine-ribose-phosphate-phosphate-phosphate. This substance, in conjunction with an appropriate enzyme, is a powerful phosphorylating agent and belongs to a class of compound which we call high-energy phosphates, because the energy released when the terminal phosphate group is split off is about 10,000 cals., as compared with the 3000 cals. released when an ester phosphate bond such as that of glucose-6-phosphate or glycerol phosphate is hydrolysed. Because of the high energy of the terminal phosphate bond, ATP can supply the driving force for the synthetic reactions involved in cell growth and is in fact the link between the energy-liberating metabolic reactions and the energy-requiring synthetic reactions. I should like to emphasise that the prime object of alcoholic fermentation, so far as the yeast is concerned, is the mobilisation of energy into molecules like ATP which can be used to drive the synthetic reactions of growth; it is not the production of alcohol and carbon dioxide, however much we may appreciate that activity on its part.

The fermentation of sugars by yeasts can be divided into four phases: (1) the passage of the sugar across the outer cell membranes into the cell; (2) the preparation of the sugar for entry into the energy-yielding mechanism; this may involve only hydrolysis as in the case of maltose or sucrose, or both hydrolysis and phosphorylation reactions in the case of lactose, melibiose and raffinose, where the galactose released by hydrolysis requires special preparation before it can enter the energy-yielding system which is common to all hexoses; (3) degradation leading to the release of energy, some of which is lost as heat and some of which is retained in the form of ATP and can be used in the fourth phase, (4) the synthesis of cell

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materials. For the sake of completeness we will also mention that in phase 3 some of the intermediate breakdown products may be tapped off and used to supply component parts of the cell structure. In this paper we will not concern ourselves with this aspect of fermentation, nor with phase 4. We shall restrict ourselves to a consideration of phases 1, 2 and 3.

Most of the naturally occurring carbohydrates fermentable by yeasts are derivatives of glucose, or of glucose and fructose. A few, such as lactose and raffinose, also contain galactose. If, therefore, oligosaccharides are first hydrolysed to their component hexoses before being metabolised further, and we have now no good reason for disbelieving this, then the yeast has to deal with only three different hexoses. With a little initial manipulation these three sugars can be modified to give the same compound: fructose-6-phosphate, and in the absence of oxygen the subsequent breakdown of this compound to ethanol and carbon dioxide supplies the energy necessary for growth.

Except for points of detail, the chemical changes which occur during alcoholic fermentation of glucose or fructose by yeast extracts have been known since 1940. Briefly, they are as follows: Glucose is first phosphorylated by reacting with ATP to give glucose-6-phosphate; this is then isomerised to fructose-6-phosphate which in turn reacts with a second molecule of ATP to give fructose-1 : 6-diphosphate. Fructose reacts with ATP to give fructose-6-phosphate directly. Fructose diphosphate is then split to give glyceraldehyde phosphate and dihydroxyacetone phosphate which form an equilibrium mixture. To reach this point two molecules of ATP have had to be expended. Now comes the first point at which synthesis of ATP can occur. The oxidation of phosphoglyceraldehyde to phosphoglyceric acid is a strongly exothermic reaction and some of the energy released in this oxidation is trapped in the form of ATP. The mechanism of this oxidation was one of the last points to be settled. It involves the transfer of hydrogen to the oxidised form of diphosphopyridine nucleotide (DPN) and the uptake of orthophosphate to give 1 : 3-diphosphoglyceric acid and reduced diphosphopyridine nucleotide. The phosphate attached to the carboxyl group of diphosphoglyceric acid is a high energy phosphate and it can be transferred to adenosine diphosphate (ADP) to give ATP and 3-phosphoglyceric. Isomerisation to 2-phosphoglyceric then occurs, with 2 : 3-diphosphoglyceric acid acting as a coenzyme. The 2-phosphate of 2 : 3-diphosphoglyceric acid is transferred to the 3-phosphoglyceric acid releasing a molecule of 2-phosphoglyceric acid and regenerating a molecule of 2 : 3-diphosphoglyceric acid. Dehydration of 2-phosphoglyceric acid gives 2-phosphoenolpyruvic acid, and in this compound the phosphate is again a high energy phosphate because of the enol configuration of the pyruvic acid. It can react with ADP to give another molecule of ATP and pyruvic acid. Pyruvic acid is then decarboxylated to acetaldehyde, which then reacts with the reduced diphosphopyridine nucleotide produced in this reaction (the oxidation of glyceraldehyde phosphate) to give ethanol and regenerate oxidised diphosphopyridine nucleotide.

The overall sequence of reactions can be represented by the equation:

$$\text{Glucose} + 2\text{ADP} + 2\ \text{phosphate} \rightarrow 2\ \text{ethanol} + 2\ CO_2 + 2\ H_2O + 2\ \text{ATP}$$

Thus although 2 molecules of ATP are used up in the initial phosphorylation steps, there is overall a net production of 2 molecules of ATP per molecule of glucose fermented.

There is an uptake of phosphate and of ADP in this series of reactions, so that if fermentation is not to stop these substances must either be supplied or be regenerated. In the intact cell they can be regenerated by utilising the ATP in synthetic reactions, or by hydrolysing it to ADP and phosphate, or by utilising it to phosphorylate more glucose and then releasing the phosphate from the phosphorylated sugar by phosphatase action. Cell-free extracts however are often

deficient in phosphatases and then the ATP phosphorylates more glucose to give fructose diphosphate. The overall equation then becomes:

$$2 \text{ glucose} + 2 \text{ phosphate} \rightarrow 2 \text{ ethanol} + 2\ CO_2 + 2\ H_2O + \text{hexose diphosphate}$$

which is the equation first suggested by Harden and Young in 1905 when they found that alcoholic fermentation by yeast extracts was dependent on a supply of phosphate.

This series of reactions, which we call the Embden-Meyerhof-Parnas glycolysis system, accounts for all the known facts of alcoholic fermentation of glucose and fructose by yeast extracts. Galactose fermentation, however, involves a few extra steps which have only finally been worked out in the last ten years. Some of the enzymes required for these steps are not synthesised by the yeast unless it has been grown in the presence of galactose. They belong to a class of enzymes which are called adaptive, or inducible, enzymes because they are only synthesised when specific compounds are present in the growth medium, these compounds usually being substrates for the enzyme or substances structurally related to the substrate.

For galactose fermentation at least three enzymes are required which are not required for glucose fermentation. (1) The first catalyses the phosphorylation of galactose to give galactose-1-phosphate. (2) The second catalyses the inversion of galactose-1-phosphate to glucose-1-phosphate and this reaction involves a comparatively new coenzyme, uridine diphosphoglucose. The mechanism of this inversion is not yet understood. (3) The third enzyme catalyses the conversion of glucose-1-phosphate to glucose-6-phosphate. This reaction requires 1 : 6-diphosphoglucose as a coenzyme and the mechanism is exactly analogous to that involved in the conversion of 3-phosphoglyceric acid to 2-phosphoglyceric acid. Of these three enzymes the first two are adaptive.

It has been found that the ability of yeasts to ferment galactose is genetically controlled and there is evidence that the presence of three complimentary dominant genes is necessary. On the basis of the Tatum and Beadle hypothesis that each gene controls the formation of one enzyme, it can be deduced that at least three enzymes are involved in galactose fermentation which are not required for glucose fermentation. Two of these enzymes could well be those involved in steps (1) and (2) above.

The fermentation of maltose, sucrose, raffinose and melibiose has also been shown to be controlled by dominant genes and in most cases the enzymes concerned are the hydrolases. Thus genes have been described controlling the formation of (1) a specific maltase hydrolysing only maltose; (2) a non-specific α-glucosidase hydrolysing α-glucosides, including sucrose; (3) invertase, hydrolysing sucrose and raffinose; (4) an α-galactosidase, hydrolysing raffinose and melibiose. In the case of maltose fermentation as many as six polymeric genes have been described, the presence of any one being sufficient to confer on the cell the ability to ferment maltose. A similar situation exists for sucrose fermentation, where three polymeric genes have been described.

As yet, no rigorous biochemical analysis has been made of yeasts which can carry out the same reaction, say maltose fermentation, but have different genes for maltose fermentation. There is some evidence that enzymes of different specificities may be synthesised according to which gene the organism contains. Thus, in presence of the maltase gene M_1 the yeast can ferment both maltose and sucrose, while in presence of gene M_2 it can ferment maltose but not sucrose.

So far we have dealt with phases 2 and 3 of fermentation. Now let us look at phase 1, the passage of the fermentable sugar into the cell. It is well known that cell membranes exhibit highly specific permeabilities. They are impermeable to most of the phosphorylated derivatives of glycolysis, sometimes to amino-acids and even to potassium and phosphate ions. It used to be thought that those substances

which could penetrate into the cell did so by simple diffusion, but recently it has been shown that for some substances this is not so. Potassium and phosphate ions for example can only pass into the cell if the organism is actively metabolising. The uptake of these substances is said to require active transport. The uptake of amino-acids and of certain β-galactosides by *Escherichia coli* also involves active transport; it is inhibited by sodium azide and by dinitrophenol, compounds which are known to prevent the utilisation of the energy of ATP for synthetic purposes. Moreover, besides requiring energy, this transport appears to be mediated by substances having all the properties of enzymes, and these transport enzymes have been christened 'permeases'. From the work so far reported it would seem likely that each permease is specific for a group of related compounds; for example, the transport of β-galactosides into *E. coli* is effected by one permease, that of certain amino-acids by another.

For yeast, only the uptake of α-methylglucoside has so far been clearly shown to involve permease action. Most of the work on this subject has been carried out with the bacterium *E. coli*, but since it is very probable that the experiences with *E. coli* will also be found with yeasts I should like to describe them briefly to you.

The uptake of β-galactosides, of which lactose is one, has been shown to involve permease action and the utilisation of lactose by this organism involves the following steps:

$$\text{Lactose (exogenous)} \xrightarrow{\text{permease}} \text{Lactose (endogenous)} \xrightarrow{\beta\text{-galactosidase}} \text{Glucose} + \text{Galactose}$$

By measuring, by independent methods, the galactoside permease activity and the β-galactosidase activity it has been found that these activities can vary independently of each other. Now mutant strains of *E. coli* exist which have lost the ability to utilise lactose, but genetic tests show that the change which has resulted in this loss of lactose fermenting ability is different in each case. On analysing some of these mutants for the presence of galactoside permease and β-galactosidase it was found that in some of the mutants this inability to ferment lactose is due to the absence of the permease, whereas in others it is due to the absence of the lactose-hydrolysing enzyme β-galactosidase. In both cases the overall result is the same, the organism is unable to ferment lactose, but in one case the reason is that the lactose cannot penetrate into the cell, whereas in the other case the lactose can get into the cell but having got there it cannot be hydrolysed.

To what extent the formation of permeases in yeasts is genetically controlled remains to be discovered. Perhaps some of the polymeric genes involved in maltose fermentation and sucrose fermentation are responsible for permease synthesis rather than for the synthesis of the hydrolytic enzymes. It has been shown that the rate of maltose fermentation by a strain of *Saccharomyces cerevisiae* is normally limited by the activity of the maltose permease, the rate of transport of maltose into the cell being the slowest step. If it should be found that this is also the case for other sugars then we have a simple explanation for the fact that oligosaccharides, particularly maltose, sucrose and lactose, are often fermented at higher rates than their component hexoses, despite the fact that they are all ultimately metabolised by a common pathway.

THE USE OF PEATLAND IN IRISH AGRICULTURE

by

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INTRODUCTION

IN ANY consideration of the land use pattern in Ireland, peatland immediately comes forward as a highly important feature. This arises not merely because of the 20 per cent or so of the national acreage covered by bogs of various types, but more especially because of the fact that in many areas it is the only soil resource available. Because of this, peatland agriculture has received very considerable attention from writers on agricultural topics, including such well-known authorities as Arthur Young, Gerard Boates, the Bog Commissioners (1809–14), Sir Robert Kane and G. H. Kinahan. It is of very considerable interest that many of the facts known over a century ago to peatland farmers in Ireland only became known elsewhere at a much later date. Indeed, much of the information contained in the Bog Commissioners' reports on such topics as drainage, peat types, use of fertilising materials, general amelioration and cropping still retains its value. For instance, the mineralisation or maturation process, which is of such great importance in peatland reclamation, seems to have been thoroughly appreciated some two centuries ago.

It is not the intention of this paper to review the very great volume of literature on what might be termed the traditional craft of peatland reclamation evolved during many centuries of trial and error. Rather is it the intention to deal more specifically with the systematic experimental fashion in which this problem is now being approached, while at the same time attempting an assessment of the craft of peatland reclamation as we traditionally know it, in terms of modern scientific findings.

OUR PEATLAND RESOURCES

A precise knowledge of the extent of our peatland resources, and more especially with reference to the various categories of peatland which occur, is lacking. There has been no comprehensive survey of bogs throughout the country for over a century, apart from the limited surveys of Bórd na Móna in connection with fuel harvesting activities. The Bog Commissioners' report (1809–14) showed that there were slightly over three million acres of peatland or bog in the thirty-two counties. This area consisted of some one million acres of low-level bog (probably consisting of raised, swamp and valley bogs). In addition there were some 400,000 acres of bog in the western maritime counties and in Co. Wicklow, with an additional estimated 1,375,000 acres of unproductive mountain bog. For the last year (1917) for which a separate heading for turf bog was included in the agricultural statistics it was recorded that the area under turf bog was 766,353 acres, with 463,297 acres of barren mountain and 339,297 acres of marsh which included substantial areas of bog. It has been estimated (by Bórd na Móna) that there are probably some 440,000 acres of bogland available for fuel production, using present modern harvesting methods.

There is ample evidence of bogland being used for agriculture for several centuries. Today relatively large areas of peatland are being used in farming in several parts of the country. From a comparison of bogland areas as shown in the Bog Commissioners' reports, and in the more recent paper by Dr. Andrews of Bórd na Móna, it is clear that during the past century or so very considerable areas

of peat have been cut away. While much of this cutaway lies derelict, in some districts appreciable areas have been converted into agricultural land.

During the present century special attention has from time to time been devoted to peatland reclamation. During the period of the First World War experiments on the manuring and cultivation of cut-over bogland for agricultural use were undertaken in Counties Kildare and Tyrone, with some very valuable results. A new approach was made to this problem when, in 1927, peatland reclamation was undertaken by the Land Commission at centres in Connemara, Mayo and Donegal for the purpose of setting up new holdings in order to relieve congestion. Under this plan some 128 holdings of approximately forty acres each were established on deep peat. Of the forty acres, two acres were reclaimed by the Land Commission, the remainder being left for attention by the allottee. For a variety of reasons this scheme did not achieve the desired results. Sizeable areas of virgin and cutaway bog were reclaimed under the Land Reclamation Scheme (1931–40) and the Farm Improvements Scheme (1940–49) operated by the Department of Agriculture. Many of these reclamations were highly successful and are being farmed at the present time.

In more recent times extensive reclamation projects have been undertaken by the Irish Sugar Company, primarily with the stated object of ameliorating peat for the purposes of sugar-beet production, with the growing of grass for drying, more or less as a pioneer crop, in the early stages of reclamation. This project was eligible under the Land Rehabilitation Project of the Department of Agriculture for a substantial grant.

Problems in Peatland Reclamation

When the problem of peatland use in agriculture is considered it will be found quite complex. This complexity arises from the fact that such main factors as peat types, social conditions, type of use (agricultural, horticultural or forestry) and so on have all to be integrated.

Peatland Types

While in recent years there has been a considerable amount of research in progress on the definition of peat types, the fact still remains that the position with regard to the classification of peats is far from satisfactory. In Ireland we are primarily concerned with two major groups of peats, the climatic or blanket peats and the raised type bogs. However, these are only broad divisions. Within each group there are various subgroups and types depending on topography, situation, climatic conditions, types of vegetation and so on. The problem here is at least equally as complex as that which arises in the classification of mineral soils.

Major subgroups which must be considered in relation to agricultural use are the raised or hochmör type bogs of the central plain, the low-level blanket peats of the western seaboard area, the high-level blanket peats of hill lands throughout the country, shallow peats constituting the A_o horizon of podsols, the valley peats constituting an important feature of the Drumlin catena in Counties Monaghan, Cavan and Leitrim, and the swamp or marsh type peats known as corcas land in many areas. Within these groups important characteristics which influence reclamation depend on botanical, physical and chemical composition, the topography of the surrounding terrain, the topography and nature of the bog floor, local climatic conditions and general situation. To consider each of these factors fully, would of itself require a very comprehensive treatment. It must suffice to mention but a few.

Physical Differences

Differences concerned with such factors as total depth of peat, stratification, degree of decomposition, moisture-holding capacity, permeability, and so on, play a highly important part in determining reclamation activities. There is for instance

a major difference in the approach to undecomposed moss peats and the highly decomposed scirpus type peats characteristic of some bogs. The residue of each particular bog plant has its own specific type of structure and texture depending on climatic and general biological conditions. Each such residue also decomposes in a specific way. Each particular type of peat is, therefore, a specific product having its own permeability and drainage characteristics. It is only through a study of these characteristics that a proper approach to reclamation is possible. Knowledge in this particular sphere is far from being satisfactory.

Type of Bog Floor

The nature of the bog floor is of primary importance in determining reclamation; a sandy permeable subsoil or an intractable boulder clay present completely different conditions to horizontally bedded rock or the A_o horizon of an iron-pan podsol. For instance, many Dutch, German and Danish bogs lie on strongly podsolised sandy subsoils, while many Irish raised bogs are on relatively impermeable boulder clay material and our blanket bogs very often on strongly podsolised impermeable soil and even on flat rock. Each of these presents its own particular problem from the reclamation aspect.

Chemical Constitution

In most accounts of peatland reclamation work, discussions on the chemical composition of peats generally refer to the quantities of nutrient elements present. However, this is not the only or even the most important aspect of the matter, as there is the equally important question of the organic composition of the peat. Eventually the manner in which structure improvement following mineralisation can be effected, depends on the reaction of the organic matter to microbiological activity and root growth effects. In this connection the types of carbohydrate and nitrogenous materials present are highly important. The rate at which mineralisation or maturation proceeds is also intimately connected with the organic constitution of the peat.

A highly important aspect of practically all peats in their natural condition, is the presence of strongly reducing conditions. However desirable this may be in relation to the availability of certain of the inorganic elements, root development under such conditions is extremely difficult. The problem of chemical composition is therefore of itself many-sided and as yet insufficiently understood. Similarly, from the biological aspect many problems arise.

Objectives in Peatland Use

From the national overall land-use aspect, the extent to which peatland can play a part in the national agricultural economy is of obvious importance. Visitors to such European countries as Denmark, Sweden, Norway, Germany and Holland are immediately impressed by the extent to which attention has been given to peatland reclamation. However, in these countries there is great pressure on the land, arising from a high population per acre of good mineral soil and a long tradition of intensive farming. Looked at simply in this way, therefore, peatland reclamation could not be considered as requiring or meriting priority in this country. However, on close examination it is seen that the problem goes much further than this. In considering this matter the following separate and distinct questions arise.

(1) It is a distinct feature of the farming and rural population pattern in Ireland that there is considerable congestion on the poor land in certain areas, especially along the western seaboard. In these areas also the main soil resource available is peatland. If the making of farmland from this bogland is economically feasible, taking both economic and technical considerations into account, it would obviously

be of distinct value as a means for the relief of the congestion which now exists. In this connection we are concerned with an important social problem which cannot be evaluated on the usual economic basis.

(2) Even in the areas of more extensive farming, there are many small farms which from the economic aspect would benefit greatly by expansion. Again in many such instances the reclamation of peatland is one of the few avenues of expansion possible. A common feature of many such areas is the presence of derelict cut-over bog-land, bordering smallholdings, which for efficient working must be increased in size.

(3) Following the introduction of large-scale mechanised peat fuel winning activities by Bórd na Móna in recent years, the problem of the best means of utilising the remaining cutaways has arisen. Much of the preparatory work in the way of drainage which has to be carried out in harvesting peat for fuel, can be geared to the after-utilisation of the bog either for agriculture, forestry or other such enterprise. On the other hand the depth to which cutting can or should proceed in order to leave a sufficient depth of peat for subsequent conversion into land, is an important factor which comes into play. Likewise the system of drainage which must be instituted for agriculture may not necessarily be that which is most suitable for drying peat for harvesting. However, suitable modifications may be possible. It is obvious that if the best use is to be made of the preparatory work necessary for peat fuel harvesting, that reclamation should take place immediately afterwards so that reversion to a scrub-like condition can be avoided. Each type of fuel harvesting activity, such as those of sod peat and milled peat, essentially presents its own reclamation problems.

(4) A large acreage of the hill land of the country is either covered by deep blanket peat or by the shallow peaty A_o horizon of podsols. At present the carrying capacity of much of this land is about one sheep per five or six statute acres, and, therefore, much below the potential to which modern agricultural technology should be capable of raising it. This then is a major category of land available for improvement once the appropriate low cost techniques have been developed.

(5) Because of the very extensive acreages available in some areas, peatland presents some possibilities for the growth of industrial crops where large-scale mechanised methods of production are necessary. At present this is almost virgin territory for investigation. An obvious use to which such land might be put is for the growth of timber for pulp and other purposes once the techniques of planting and general culture are mastered. The present Forestry Division investigations in this respect show much promise. If these are finally successful, there will arise the necessity for the integration of agriculture and forestry in certain areas, as from the labour employment and general social point of view, these two enterprises have many complementary aspects.

(6) There finally arises the question, following the development of new improvement techniques and of the appropriate machinery, if peatland farming as such can be practised on a sound economic basis.

Because of the need for a thorough investigation of the many aspects of this problem using modern scientific techniques, investigations have been undertaken and are now in progress at a number of centres by this Department. Two main aspects of the problem are being examined: (1) the reclamation of deep blanket peat and (2) the conversion of cutaway peat into farmland following Bórd na Móna activities. The former is being investigated at the Peatland Experimental Station, Glenamoy, Co. Mayo, and the latter at the Peatland Experimental Centre, Derrybrennan, Co. Kildare, with a sub-centre at Clonsast, Co. Offaly.

Experimental Work on Blanket Peat

The Peatland Experimental Station at Glenamoy in North-West Mayo was founded some two years ago as a main centre for experimental work on the utilisation

of blanket peat for agriculture and other related purposes. At this centre a comprehensive programme of investigations is now under way. These include: (*a*) investigations on such matters as drainage, methods of cultivation, cropping, manuring, livestock husbandry and farm management; (*b*) investigations on the improvement of the native sward through such practices as over-seeding, liming, manuring and grazing, with the ultimate objective of developing a low-cost technique capable of achieving a substantial increase in output from such land; (*c*) investigations on the production of industrial crops.

Peat Type, Vegetation and Climate

The peat is typical of that of low-level blanket peat along the western seaboard, varying from four feet to twenty feet in depth and situated at an altitude varying from almost sea-level to two hundred feet. The surface is gently to moderately rolling, rising to two domes at the highest points. A detailed survey of bog depths and floor contours has been carried out as a basis for the work. The peat lies directly on disintegrated mica-schist, the topmost portion of which consists of a strongly podsolised iron-pan podsol. H values (Von Post) vary from 5–6 in the surface to 9–10 at lower depths. Detailed chemical analysis on two profiles representative of the area have been carried out (Walsh and Barry, *Proceedings of the Royal Irish Academy*, in press). These show in general a low ash content (1·2 to 2·6 per cent), moisture 93 per cent, pH 4·7, nitrogen content 1·5 per cent, with very low levels of calcium, potassium, phosphorus and other mineral elements. The trace element position is of particular interest, with very low levels of molybdenum (0·40 p.p.m.), copper 5–8 p.p.m. cobalt 0·50 p.p.m., with other trace elements such as tin, nickel and vanadium also low. Lead, at 6·0 to 9·1, p.p.m., is at about the same level as copper. While there is a more or less full range of bogland plants represented in the vegetation, *Schoenus nigricans* is dominant, with *Eriophorum vaginatum* co-dominant over a considerable portion of the area. The area is completely devoid of shelter. In the bog pools which are a feature of this and other blanket peats in the surrounding area, *Menyanthes trifoliata* and *Eriocaulon septangulare* dominate. Many species of *Sphagna* are present on the wetter areas near the pools, with *Cladonia* on the drier areas.

Climate

The average rainfall is fifty to fifty-five inches, with some 270 rain-days in the year. As the area is very exposed, gale-force winds are experienced.

Drainage

Because of the present lack of understanding of the many difficult moisture relationship problems of peat, the question of drainage is being approached with considerable caution. A large-scale drainage experiment, including such aspects as distance apart and depth of drains, efficiency of mole drainage, lateral movement of moisture, surface run-off, loss of moisture through evaporation, cropping and drainage, soil temperature and biological activity in relation to moisture and structure development, is under way. Apart from this specific experimental work, a considerable volume of information has been collected from observations following the general drainage of the area by drains at fifty feet apart. It has been found through systematic observations made in bore-holes placed at intervals between the drains that the lateral movement of moisture is very slow, the moisture status of the peat being affected to an appreciable extent only to a distance of two to three feet on each side of the drain. This also leads to differential shrinkage and sets a number of problems in cultivation and cropping, apart from difficulties in drain maintenance. Experience with drain spacings at one hundred feet apart has shown that this or even a greater spacing may be satisfactory. In the initial stages of drainage a Cutbertson B-type plough (drawn by two Platypus tractors in tandem) was used,

and in later work a plough specially designed by Bórd na Móna, which has the distinct advantage that it is much lighter than the conventional type deep-drainage ploughs, has been used to advantage. This system of drainage is by and large a very low cost one. The experience has so far been insufficient to allow of any valid comment on the problems of drain maintenance. It is basic to the whole problem of drainage that more precise information be available on water movement and behaviour in peats of the type under investigation.

Cultivation

When it is realised that the moisture content of the peat practically to the surface may be over 90 per cent, it can be seen that in the early years of reclamation, cultivation sets particularly difficult problems. In general, for the growing of cereals and grasses, a technique has been evolved which consists of discing and rotavating to a depth of about 4 inches, with the thorough incorporation of fertilisers and lime into this zone. This has been found to be the minimum depth necessary to ensure adequate root development. With the exception of oats, root development has been confined to this zone. In a dry period such as occurred in June of 1957, barley and kale showed symptoms which suggested drought conditions in this shallow rooting zone, despite the fact that a few inches below, the peat contained 94 per cent moisture. In order to facilitate quick run-off of excess surface moisture to allow of cultivation and sowing, it has been necessary to adopt a system of gentle cambering from the edge of the drain towards the centre of the plot. This has, however, the disadvantage that it also leads to surface washing-off of ground limestone and fertilising elements. These conditions refer specifically to the sowing of crops within a year or two after first opening the drains. It cannot be overemphasised that special attention to cultivation techniques is absolutely necessary, and much more so than in the case of mineral soil. At present the system of cultivation practised is relatively costly, especially for the growing of cereals, but in time, with the development of the appropriate equipment for combine drilling and harvesting, it is hoped to decrease costs to a level comparable with those for mineral soils. In general it can be stated that a serious impediment to cultivation rests in the non-availability of machines suitably adopted to peatland conditions. It is a specific objective of the work in progress to develop suitable mechanical equipment to deal with the situation.

Chemical Characteristics and Manuring

It is the general experience that the mineral fertility of peat soils, especially that of the upper layers, is extremely low. The relatively low levels of nutrients in the peat at Glenamoy, as shown by the analyses, have been amply verified in the crop response results to date. In using chemical analysis of peats as a basis for manuring, entirely different standards must be used than for mineral soils, not only because of the differences in the nature of the materials involved, but also because of the very confined depth of rooting. It is of obvious importance to establish such standards and attention is being given to this matter.

Experience on manuring to date has shown phosphorus and nitrogen deficiencies to be especially severe, with also a distinct response to potassium on grass swards as reflected in the growth of clovers. For such crops as cereals, grass and kale the application of nitrogen at relatively frequent intervals throughout the season has been found to give the best results. With kale, striking responses have been got from a total application of up to 10 cwt. per acre of nitrogen as fertiliser. At least this quantity is necessary for best results in the early years of reclamation. Different sources of phosphorus such as superphosphate, basic slag and rock phosphate have been used with equal success. In the case of the latter, however, when applied in conjunction with ground limestone the availability has been shown to be distinctly

reduced. While potassic manuring is necessary, it may be pointed out that both the potassium and sodium contents of the peat at Glenamoy are considerably higher than for bogs situated inland and more removed from sea influence.

Experience so far has shown that trace-element problems are of particular importance under the conditions at this centre. First attempts to grow cereals ended in failure to produce grain, despite relatively generous general manuring and liming. Subsequent investigations have shown copper deficiency to be the major cause of this, and very spectacular results have been got from the application of copper to oats and barley. During the past season relatively satisfactory crops of these cereals have been obtained, where copper was used following a period of only two years of drainage. The optimum dressings of copper sulphate to the soil has been found to be 28 lb. per acre, with 10 lb. applied as a spray also giving good results. Table I below summarises some of the results obtained for oats and barley.

TABLE I

(Showing yield (cwt./acre) from copper application)

Copper sulphate applied (lb.)	0	28	56	10 as spray
Oats (Castleton)	3·6	18·5	22·8	18·3
Barley (Herta)	14·8	25·9	24·7	27·0

Distinct varietal differences have been obtained in response to copper, varieties of cereals from peatland and other areas in several European countries having been included in the investigation. The best yields so far obtained have been 29·3 cwt. per acre of oats from the variety Marne, and some 29·1 cwt. of barley from the variety Herta. These compare favourably with those obtained on many mineral soils under normal farming conditions.

This capacity to produce cereals is of particular importance in view of the role of these crops in the early years of a mixed farming enterprise. Experiments on other aspects of copper response, especially on grassland, are now also under way.

For some crops, striking responses to molybdenum have also been obtained in pilot experiments. Without the use of this element complete failure of such garden crops as lettuce and cauliflowers has resulted, with striking responses also being obtained in the case of a number of other brassicas, peas and other crops. The significance of molybdenum under these conditions for a number of other crops, especially clovers, is now also being investigated. Boron deficiency has been particularly severe in turnips, with symptoms also identified in kale. Another distinct feature of crop response is the occurrence, in the absence of liming, of a distinct intervenal chlorosis in cereals, grasses, and, following fertiliser application, in such native herbage as *Molinea caerulea*. This chlorosis has occurred mainly near drains and seems to be related in some way to aeration. It is thought that it is mainly due to heavy-metal toxicity, possibly associated with increased acidity following aeration. It is eliminated by liming.

Liming

The use of lime on this peat presents especially intriguing problems. It is generally thought that *Schoenus nigricans*, which dominates the native herbage, is an indicator of moderately satisfactory base status condition. Chemical analysis, however, in general shows a pH of about 4·7, with low levels of calcium. Experience so far shows that while in the early weeks of pasture establishment there is a distinct response to lime, even at levels as low as 10 cwt. of ground limestone per acre, in a short time the difference almost disappears. At high levels of lime

on newly established pasture there was a distinct depression of clover growth. With cereals and other crops a response to ground limestone was noted, this also being the case in experiments on the improvement of the native sward by overseeding. It is, however, too early as yet to give a definite liming programme for this peatland. Detailed investigations are now under way on such matters as the most efficient method of lime distribution and incorporation into peat, loss of calcium through bleaching, value of different fineness grades of ground limestone, the response of different crops to lime and its effect on the availability of nutrients, both major and trace.

Amelioration of Peatland

Practically all accounts of peatland reclamation emphasise the importance of achieving, in the shortest possible time, a conversion of peat from the reduced state in which anaerobic decomposition is the dominant process, to a mineralised material properly aerated and humified. This process depends on a great many factors associated with both physical, chemical and biological conditions. Various techniques involving the application of sand, gravel, or other ameliorants are generally resorted to, to achieve or aid this mineralisation. In order to obtain information on this process a thorough study is being undertaken of the various chemical and biological processes involved, beginning with a study of the different organic materials present in the peat. The effect and degree of this process of mineralisation on nutrient availability is also being studied.

General Farming of Peatland

In order to explore various aspects of peatland farming, both economic and technical, a pilot experimental farm has been set up. This consists of some hundred acres for farming, together with forty acres of shelter belts suitably arranged. Because of the exposed conditions at this centre, the provision of shelter is of special importance. The impact of these shelter belts on wind velocity and other climatic effects is being fully recorded from an early date. At a later date experimental work on the value of the shelter belts, for sheep and other stock, will be integrated with the farming system. In farming peatland many special problems are involved. Because of the moisture content of the peat and its physical nature the grazing season is much more limited than for free-draining mineral soils. To meet the situation special measures in the way of housing and the provision of fodder are necessary. The farm buildings have been erected on deep peat, using a raft technique specially developed for the purpose. In this respect valuable experience has been obtained. Much of the winter feeding programme is being based on silage as it is a primary objective to have the farm self-sufficient to a high degree. Several other aspects of farm management, including the breed and type of livestock most suited, on an economic basis, to the conditions, are receiving attention. There is a full costing of this project.

Special problems in grassland management arise. These are concerned not only with the development of information on the most suitable species of both grasses and clovers, but also with the impact of the herbage on the animal. It has been shown that the peat is deficient in copper and cobalt, both highly important for ruminant animals. This unique opportunity is consequently being availed of for the investigation of several aspects of the significance of these elements in relation to animal health. Investigations on the mineral status of various components of the native sward such as *Schoenus nigricans* are also under way. This is of special significance in relation to hill-farming problems.

Hill Land Improvement

As herbage and general grazing conditions are typical of those for large areas of hill and marginal land along the western seaboard and in other parts of the country,

experiments have been undertaken for the purpose of developing suitable techniques for improving the native vegetation at low cost. The land at Glenamoy previous to reclamation carried sheep at the rate of about one per six or seven acres, this being typical of a very considerable area of these waste-lands. The results of the experiments to date show that with proper use of phosphatic fertiliser, coupled with liming, a good clover sward can be established on the surface without cultivation by overseeding. Striking differences in response effects between nitrogen, phosphorus and potassium have been shown. Again many problems arise not only from the aspect of determining the minimum quantity of phosphatic fertiliser and lime which will suffice, but also the effect of this improvement on the native vegetation and on the animal. From the results obtained to date there would seem to be a distinct possibility of being able to develop low-cost techniques capable of enabling a very substantial increase in the carrying capacity of bog and mountain land.

Industrial Crops

Experiments are now in progress on the growing of bamboo as a source of wood pulp, New Zealand flax and hemp for fibre, grass for drying, and potatoes for starch. Some fifteen species of bamboo are under investigation, but this is essentially a long-term investigation. Pilot trials on the growth of cranberries, blueberries and other related fruits have also been established with a view to possible use as commercial horticultural crops on peatland.

Reclamation of Cutaway Bogland

As noted previously, very large areas of peat have been cut over during the past century or so and a considerable area of the resulting cutaway lies derelict. There are many types of cutaway peatland, as there are variations in the type of peat and cutting process. Various methods of harvesting peat by hand have been operated, depending on the type of peat and the district. Generally the traditional procedure has been to remove the topmost fibrous very acid layer to the depth of a yard or so and to deposit this on the old cutaway, thereby leaving this fibrous material for soil-making purposes. While in some countries this has been adopted as the best method as a basis for reclamation, under Irish conditions it has been more a method to get rid of the unwanted topmost fibrous material, in order to get at the underlying peat for fuel, rather than one specially designed to give a good soil later.

The depth to which peat has been cut over naturally influences very much the value of the cutaway for conversion into soil. In many parts of the country cutting over down to practically the subsoil level or rock has been practised, especially in areas where fuel is scarce. Where there is a permeable sandy subsoil, this technique in fact may have much to recommend it. However, as the subsoil of much of the raised bog is either of an impermeable intractable nature or consists of highly calcareous marl, too severe cutting presents very difficult reclamation problems. There also arises the question of the relative merits of the different peats, such as reed peat found near the bog floor, as soil materials. Further, because of the process of oxidation and mineralisation, which may cause rapid shrinkage of peat, there arises the major problem of the most satisfactory moisture-level for peat soils.

These problems and many others, especially those associated with the method of fuel-winning (sod or milled peat) have come particularly to the fore in recent years following the large-scale fuel-winning activities of Bórd na Móna. To investigate these problems experimental work has been started at Derrybrennan, Co. Kildare (milled peat system) and at Clonsast in Offaly (sod peat system). Again only preliminary results from three years' work at Clonsast and one year at Derrybrennan are available.

Clonsast

At this centre a crop rotation trial investigating response to lime of oats, kale, potatoes and grass at different levels of fertiliser is in progress. The cut-over is residual from sod peat winning activities which are more or less similar to the traditional method of throwing the top undecomposed surface layer to a depth of about a yard, on to the cut-over surface. The area was prepared for experimental work by levelling over the surface, and due to variations in peat type and depth of cutting, this meant that the topmost layer of the cut-over was not by any means uniform. Here and there the more decomposed fen type, *Carex–Phragmites* derived peat, came close to or was actually at the surface. As a soil parent material this peat, derived from the machine cutting and mixing activities and with contamination from the lower peat, was relatively heterogeneous. In general, it was extremely acid except on the fen type peat areas, being very deficient in phosphorus, potassium, calcium and in a number of trace elements. Crop-growth over the area was somewhat uneven, especially on the area where the fen type peat came close to the surface. Here growth was much more vigorous than where the topmost fibrous peat was being cropped.

Response to Liming

All crops have responded strikingly to liming. The effect on oats has been particularly striking, with the elimination of a very severe intervenal chlorosis which it now seems may be due to heavy-metal toxicity under the influence of acidity. In this respect it is of interest that Walsh and Barry have recorded a much higher level of lead and nickel on peats of this type than on blanket peats. The occurrence of this chlorosis is a common feature in the early stages of peatland reclamation and has been an important cause of crop failures under these conditions. Lime deficiency effects are much more severe than on the blanket peat conditions at Glenamoy. From the results to date optimum effects have been obtained from dressings of ground limestone at between two and three tons per statute acre. This can be seen from the data in the diagram showing the yield results for the cropping year, which also gives information regarding the effect of ground limestone on the pH of the soil.

Nutrients

Without phosphorus, growth was extremely poor for all crops. Nitrogen deficiency was also acute, while there was also extreme potash deficiency. Where the three major elements were applied, there was no added effect from farmyard manure. No response was obtained to sulphur. There was, however, a distinct response to magnesium as shown in the absence of deficiency symptoms for kale, potatoes and to some extent for oats. A notable feature has been the very disappointing results for oats as far as yield of grain is concerned. This was mainly due to copper deficiency. In general, with adequate manuring and liming, crop and grass yields at least equal to those average for mineral soils have been obtained.

Moisture Study

At this centre during the first year of cropping, a system of irrigation was installed. Bore-holes were placed at suitable distances between the irrigation channels and a daily record kept of water-table height. While the water-table in the channels was maintained at a level of eighteen inches from the surface, in general in the bore-holes it was 2 feet lower than in the irrigation channels, except within the two or three feet immediately adjoining the latter. It was shown distinctly that the lateral movement of water through the peat was very limited. Despite this, however, there seemed to be some effect from irrigation on crop growth, as during the year in which irrigation was practised growth was more uniform, and yields at the same

level of manuring, were much higher than in subsequent years. This aspect of the problem remains as yet to be fully explored.

Frost Damage

Frost damage was particularly severe in the first year, with almost complete elimination of the sown species of grasses and clovers, especially ryegrass.

Peatland Experimental centre, Derrybrennan

The introduction of the milling system of fuel harvesting by Bórd na Móna has set new and distinct problems in peatland reclamation. In this system successive layers of peat, beginning with the surface, are milled and harvested until cutting has reached that depth where a suitable layer of peat remains for conversion into land for either agriculture or forestry. In some circumstances the presence of timber in the lower levels of the bog determines the depth to which cutting can be carried out. Where timber is absent the depth of cutting will depend on a great many factors, such as the type of peat and bog floor. Where cutting can proceed in a normal way on a raised bog, the layer which remains consists of peat which has widely different characteristics to that available from traditional system of cutting. It is likely to be much more decomposed and on drying much more prone to irreversible drying. Generally it will have a much higher base content, be less permeable and have a completely different chemical and biological regime than the surface undecomposed peat. Very distinct problems, therefore, arise in connection with the depth of peat which should be allowed to remain for conversion into soil and the height of water-table or drainage system which must be introduced to suit the conditions obtaining.

For the purpose of investigating some of these problems the Peatland Experimental Centre at Derrybrennan has been established. As yet in the early stages of development, the work has clearly presented many problems associated with the cut-over area remaining after milling. There is also an area corresponding to low moor peat which at one time was cultivated but is now derelict. There is also available, for comparative studies, an area of mineral soil carrying impoverished grassland, this soil being representative of an extensive area of grey-brown podsolic soils. From the investigations being undertaken it is hoped to obtain information on some of the specific problems associated not only with peatland farming as such, but with the more general problems existing in the Midlands of peatland and mineral soils combined in varying proportions.

While yet in its early stages, the study has already raised a major problem in connection with the nutrition of cereals on an area where milling has been carried out to within a depth of some four feet from the bog floor, at which depth timber intervened to prevent further cutting. At this depth the peat is still very acid. So far it has been impossible under these conditions to obtain a satisfactory crop of cereals despite adequate lime and fertiliser use. Under similar conditions it has been possible to establish a very satisfactory crop of strawberries with optimum liming at about two tons of ground limestone per statute acre. It is thought that the effect on cereals may be due to the presence of some specific organic materials in the woody type peat being dealt with. Experimental work on the herbage of the low moor (similar in many respects to a very large area of derelict cutaway peat) has shown that the speed of change in herbage composition may be very rapid, phosphorus and potassium playing a specially important part in this change. On this low moor area, also, very satisfactory crops of cereals have been obtained with also a good response from hemp.

At this centre a comprehensive programme of experiments on the problems of moisture, drainage and fertiliser use is now in course of development. Particular stress is being laid on the rehabilitation of old cut-away, a category of land which,

if it could be brought into production on an economic basis, would mean much in terms of increased productivity and more efficient farming. The high capacity of such land to produce good crops when reclamation is approached along scientific lines has already been demonstrated.

General Discussion

From the foregoing generalised account it can be seen that the use of peatland in agriculture presents many complex problems, not alone of a technical but also of a social, cultural and demographic nature.

Experience to date points to peatland farming as requiring especially high qualifications in the farmer, as the building up of fertility and the general arable, grassland and livestock farming of peatland is much more complex than the farming of mineral soil. There are problems of moisture control and subsidence, rapid mineralisation being specially important, while rapid degeneration takes place with the minimum of neglect. Success can only be achieved with constant attention to manuring and cultural operations. The cost of reclamation and subsequent farming operations demands intensive farming with a high return per land unit and per worker. In this connection there is as yet little precise information on the optimum size of holding required for any particular type of farm enterprise on peatland, in order to give the farmer a reasonable living. There is, moreover, very little information on the farm facilities, machinery and tools best suited to the special conditions operating. Because of all these factors, land settlement on reclaimed peatland obviously demands special consideration.

Broadly, the objective at present being worked to, apart altogether from a consideration of the minor achievements to date, is the development of soil and water use practices and the appropriate crop types and stock, which will allow of the farming of peatland as a normal efficient process. The growing of crops likely to act as a basis for industrial raw materials has, in view of modern trends in utilisation research, many obvious attractions for peatland and other waste-land areas. If such areas can with the appropriate type of mechanisation be brought to grow crops which modern industry can use, a considerable advance will have been made. The possibilities are sufficiently attractive to merit thorough explanation.

Apart altogether from the question of reclamation of peatland for conversion into farms, there remains the problem of the extensive areas of shallow peat and hill land to be considered. While these are now in general of very low economic value to the nation or to the holders, results of the investigations already available point to a much greater potential, especially for sheep-rearing, if the processes which we now know as being capable of giving improved grazing on such lands can be operated and developed on a low-cost basis.

Sir Robert Keane over a century ago stated that there were a few areas of the waste-lands of the country outside the bounds of agricultural enterprise. With the scientific information now becoming available on the utilisation of the various categories of peatlands and other wastelands, there is every reason to believe that this objective can be realised. Already within a very short time, using the precise scientific experimental approach outlined, the solution of many of the more difficult practical problems is in sight. It is basic to this approach that the appropriate scientific information be available. Already in recent years, research on problems relating to peat formation, peatland ecology and peat chemistry, has brought forward much new information of very great value to the agriculturist. One can only look forward to the time when, with an increase in the flow of this information, peatland reclamation can proceed in a well-ordered fashion and on a fully economic basis.

THE INFANT ANIMAL

SECTIONS I (Physiology and Biochemistry) and M (Agriculture) devoted the morning of September 10, 1957, during the Dublin Meeting of the British Association to a joint discussion on 'The infant animal'. Dr. R. A. McCance, C.B.E., F.R.S., and Dr. Elsie M. Widdowson, of the Medical Research Council Department of Experimental Medicine, University of Cambridge, presented a paper on 'The physiology of the newborn animal', which is printed in full below. I. A. M. Lucas and G. A. Lodge, of the Rowett Research Institute, Aberdeenshire, then dealt with 'The nutrition of young pigs'. They were followed by Dr. J. H. B. Roy, of the National Institute for Research in Dairying, Shinfield, with a contribution entitled 'The nutrition of the early weaned calf'. Abridged versions of these two papers are printed below.

PHYSIOLOGY OF THE NEWBORN ANIMAL

By Dr. R. A. McCance, C.B.E., F.R.S., and Dr. Elsie M. Widdowson

We have all been born, most of us have reached maturity, and some of us, alas, are approaching senility. We have all got to die, and if people are to do all these things gracefully they must make great physical and mental (Rudd, 1957) adjustments to meet the changes which are inevitable in the world around them. We have now to consider the newborn animal and its response to the exigencies of its environment—in other words, its physiology.

In some respects the newborn animal has all the characteristics of its parents, but in others it is unlike them, and both the similarities and the differences have an important bearing upon its well-being. The differences in body-size are obvious, but there are many internal differences, such as in the function and relative size of the organs (McCance & Widdowson, 1955), the activity of ductless glands, and the development of the enzyme-systems (Himwich & Fazekas, 1941; Jones & McCance, 1949), which will be mentioned later. The extracellular fluids, or, as Claude Bernard put it, *le milieu intérieur*, need a word to themselves. At birth these fluids resemble those of the adult in osmotic pressure and general composition, but their

TABLE I

Effect of giving Salt to Starving Newborn Piglets on the Katabolism of Body Protein

	Given water 240 ml. per kg. per 24 hr.	Given saline 240 ml. per kg. per 24 hr.		
		0·5%	0·7%	0·9%
Visible water balance (ml. per kg. per 24 hr.)	0	+108	+144	+193
Estimated volume of extracellular fluids (volume at birth=100) .	100	130	140	153
Nitrogen appearing as end-products (mg. per kg. per 24 hr.)	213	196	123	95

volume, relative to the volume of the cells and the weight of the body, is much greater. This has been surmised for many years on the basis of the determination of the quantity of chloride in the body, but it has become more certain since methods were developed for the determination of the volume of these fluids in living animals, including man (Flexner *et al.*, 1947; Friis-Hansen, 1954). Hitherto no function has been assigned to the large volume of the extracellular fluid in the developing organism, but work we have been doing has enabled us to make some interesting observations about expanding it still further. By adding a little too much salt to the food of babies and newborn piglets, we have produced extensive enlargement of the extracellular fluids, and some increase in their osmotic pressure (McCance & Widdowson, 1957). The result, in piglets at any rate, has always been to reduce the katabolism of protein below that of a control animal given no salt, and this has been true whether or not the animals were being fed (see Table I). Why expanding the extracellular fluids should reduce the katabolism of cellular protein remains to be discovered, but the fact does suggest that a large volume of fluid may have a functional value for a developing organism, for anything which reduces cellular katabolism will tend to promote growth.

The New World

Consider for a moment the physiological upheaval of birth and the problems which face the animal in its new environment. Before birth mammals live in the dark, surrounded by fluid at a high and uniform temperature. They are provided through a piped system with all they need in the way of food, water, air, and drainage, and get on very well without having to make any use of the organs designed to provide these services after birth. But when the cord has been cut each of these organs has to come into action at the appropriate time and take over the function for which it was evolved. Furthermore, the animal now finds itself in a new world, surrounded by air, faced by the risk of cold, of infections, of partial or complete failure of its hitherto untried organs to meet its needs. Each species has its own particular problems and solves them in its own particular way, and one of the detailed interests of infant physiology is to study how the problems which face each species in a state of nature have been solved. There are, however, ways in which all newborn animals resemble each other and differ in these respects from adults, and these general principles are the basis of infant physiology.

Protein Transfer

Although infectious diarrhoea has probably killed more infants than any other single cause, the newborn infant does not as a rule succumb to any of the great killing diseases of later childhood. It is, for the time being, immune.

The basis of an adult's immunity is the reaction of its own cells to penetration of protein from an outside source. The response consists in the development of a highly specific substance, generally termed an antibody, which is capable of making the invading protein harmless. The immunity, once acquired, may be permanent, whether or not its development has been accompanied by any signs of disease. The newborn animal has not reached the physiological stage of development to react in this way, and would be at the mercy of many of the noxious organisms in its environment, were it not protected temporarily by antibodies which have been made by its mother and transferred to it ready-made. This protection lasts, or should last, until the young animal has reached a state of maturity at which it can deal with the production of its own antibodies.

Some young animals acquire their immunity before birth and others after birth, and the routes by which these protein antibodies of high molecular weight pass from mother to young are perplexingly diverse (Brambell *et al.*, 1951; Brambell, 1954, 1955–6; Brambell & Hemmings, 1954). The rabbit, the guinea-pig, and man

acquire this passive immunity before birth. Little is known about how this transference takes place in the last two species, but the path of the antibodies from the maternal to the foetal rabbit has been mapped out by Brambell and his associates. Surprisingly enough, they do not pass through the placenta but reach the foetus from the uterine cavity via the endodermal lining of the yolk-sac and the vitelline vessels. Antibodies made by the rabbit pass into the foetus from the uterine cavity much more readily by this route than those made by man, the guinea-pig, dog, horse, or cow (Batty *et al.*, 1954; Brambell & Hemmings, 1954). In ruminants, horses, and pigs, the young are born unprotected and without any maternal antibodies in their tissues; but the colostrum of the mother contains antibodies in great quantities, and the health and survival of the newborn animal depends on them. These large protein molecules are absorbed through the cells of the gut in the first hours or days of life, and find their way thence to the lacteals and so to the larger lymphatics and the thoracic duct (Comline *et al.*, 1951*a*, *b*, 1953), without undergoing any alteration or destruction by the digestive enzymes on the way. In the mouse, rat, and dog, some antibodies are transferred before birth, and the route is known in rats. Transference after birth, however, is more important in these species, goes on for some time and does not end in the rat until the twentieth day of life (Halliday & Kekwick, 1957).

The discovery of the routes by which these large protein molecules reach the developing animal unchanged has tended to emphasise species-differences, but there are generalisations behind them of interest to all students of infant physiology. Their passage, for example, always seems to be across or through endodermal cells—of the yolk-sac or of the gut or both (Brambell, 1954)—and antibodies are almost certainly not the only proteins which pass through these endodermal membranes (McCance, Hutchinson, Dean, and Jones, 1949), though albumins seem to pass with difficulty, at any rate in the rat (Bangham & Terry, 1957*a*). Other membranes and cells, moreover, may be permeable to proteins at the appropriate stage of development (McCarthy & McDougall, 1953; Brambell & Hemmings, 1954), and passage of these proteins may be highly selective at some sites, but relatively non-selective at others (Bangham & Terry, 1957*b*; Hemmings & Oakley, 1957). So far only the passage of antibodies has been studied to any great extent, but this transference of macromolecules from mother to young must be a matter of general importance to the physiology of the young animal. In one of our litters the serum-protein of a newborn piglet was 2·3 g. per 100 ml. At 40 hours it was 2·5 g. in a piglet given nothing, 2·6 g. in one given water only, 3·0 g. in one given sow's milk, and 5·3 g. in the one given sow's colostrum and milk.

Maintenance of Homoeostasis

Ever since Claude Bernard enunciated his famous dictum, the constancy of the internal environment has been widely regarded as one of the hall-marks of mammalian efficiency. The whole physiology of the adult is directed towards maintaining a constant internal temperature, blood-sugar, hydrogen-ion concentration, and plasma and extracellular-fluid volume, and (perhaps above all) a continuous supply of oxygen to its tissues. The activities of practically all the organs are integrated to these ends, and, when the system is subjected to a strain under which it breaks down, functional efficiency falls off and the prospects of survival diminish. It has been known since the work of the pioneers (Edwards, 1824, 1832) that newborn animals cannot maintain the same internal stability as their parents. But they are also surprisingly indifferent to the resulting abnormalities in their body-fluids, and can survive changes in their own bodies and in the world around them which would be lethal later in life. To a large extent the ability to maintain stability depends upon the degree of development at birth, but for physical reasons some aspects of it are facilitated by a large size. This is one of the reasons why

the newborn is at a disadvantage compared with its parents, and the smaller species of adult animals do not exhibit the same stability, in some respects, as larger animals such as the dog and man (Gellhorn, 1937; Blood *et al.*, 1946). Indeed, the mature rat and mouse make an interesting comparison with the newborn puppy and even with the newborn baby.

Response to Cold Surroundings

A small size and a large surface make the control of temperature difficult, and some animals which are born in a very undeveloped state have no control over their body-temperature but are indifferent to considerable and protracted departures from the maternal norm.

The newborn rat is poikilothermic, and its oxygen-consumption falls as it cools (Adolph, 1948; Fairfield, 1948). The same is true of the newborn mouse (Fitzgerald, 1953). These animals, therefore, are incapable of maintaining their body-temperature when they are isolated from their mother and their littermates, but these are not their natural surroundings. Animals in a litter, huddled together in their nests with their mothers, have temperatures as near 37°C. as makes no matter (Edwards, 1824); if their mother does leave them for a time to get food for herself and their temperature falls, their uptake of oxygen and their rate of metabolism fall, too, and these poikilotherms can probably survive for a longer period of time without food than they could have if their temperature had been maintained at 37°C. Their weakness becomes a menace to their survival only if their mother fails to return to them with warmth and, after this has done its work, food. Puppies and kittens are almost poikilothermic at birth. They may have some small degree of temperature-control, but, like rats, birds, and many other newborn creatures, they depend on the warmth of their nests and their mother for their well-being. It has been known for many years that they recover satisfactorily after an extensive fall in body-temperature, but how the fall affects their survival-time, its limits, and the cause of death, have not been fully investigated. The development of every newborn animal, be it a rat or a man, depends on the mechanisms responsible for its body-temperature not being over-taxed. The newborn pig is not poikilothermic, but its body-temperature is not so stable as that of an adult. It will survive and even grow well in a cold environment provided it is regularly fed, but its metabolism, like that of most homoeotherms, is stimulated by a cold environment. Its well-being in nature is certainly facilitated by the warmth of its mother and the proximity of its littermates. If the newborn pig is not fed it can maintain its temperature reasonably well, and in a warm environment the unfed newborn pig will live comfortably on the food-supplies within its body for at least 2 days. In cold surroundings, however, the internal supplies of available carbohydrate fail much sooner. This may be due to thyroid exhaustion or a decline in adrenal activity or to many other things, but in any event the animal's blood-sugar falls rapidly, and unless glucose is administered, its body-temperature falls also, and it dies in hypoglycaemia (Morrill, 1952; Goodwin, 1957). The fall of temperature, due to the deficiency of metabolisable carbohydrate, may postpone death for a short time, but the beneficial effects must be small compared with those in a well-fed poikilotherm or (see later) in an animal deprived of oxygen.

The newborn baby is so much larger than the newborn rat or puppy that, if only for this reason, control of its body-temperature is much easier. It is not poikilothermic but, like the piglet, can tolerate a considerable fall of body-temperature below the normal 37°C. provided the return is made within a reasonable time. One of its more insidious enemies, however, is long-continued exposure to cold (Mann & Elliott, 1957). Babies born in very cold weather in homes that are inadequately heated are sometimes admitted to hospital suffering from the effects of this. By the time these babies reach the eye and the touch of an expert, they may have passed

from a physiological to a pathological state, and present with some superadded infection. They always feel cold, but in spite of this they may appear surprisingly well, with red face and hands. Sometimes the external cold has made the extremities oedematous and the skin hard and white. The protracted exposure lowers their body-temperature internally and makes them apathetic and unwilling to take food, and perhaps because of this they sometimes have blood-sugars low enough to cause convulsions. They may die before or during treatment from what appears to be respiratory failure, and pulmonary haemorrhage has often been found after death. Experiences with the newborn pig indicate that in resuscitation the administration of glucose in quite large amounts should precede the application of heat.

Control of body-temperature is not a simple process. It is not merely a question of available glucose. It cannot take place properly, before the nerve-centres in the hypothalamus are co-ordinated (Reynolds, 1953), but there is much more in it than that, and workers in Prague have shown that the activity and responses of the thyroid gland, the breakdown of glycogen, the growth of fur and other mechanisms, all begin to participate at their appointed time. Young rats, aged 21 days, can maintain their temperature much better during a first than during a second exposure to cold (Hahn, 1956*a*, *b*, *c*, *d*; Hahn *et al.*, 1956) and this has some parallel in clinical experience (Jonxis, 1957).

Response to a Lack of Oxygen

When a baby is born, the transition from uterine to atmospheric respiration does not always go as smoothly as one could wish (*Lancet*, 1957). The resistance of newborn animals to anoxaemia is, however, great (Adolph, 1948), and some anaerobic metabolism may persist functionally after birth, even in man (Gonzales & Gardner, 1957). The whole matter has been the subject of experiment since the time of Boyle (1672), and there are many records of healthy infants being born alive up to 20 minutes after the death of their mothers (Harvey, 1651; Hellman, 1953). Kittens, too, have been delivered in good shape after their mother had died of anoxaemia (Fazekas *et al.*, 1941), and it is common knowledge that these animals are exceedingly difficult to drown. When adult dogs are suddenly deprived of oxygen, their blood-pressure, their respiration-rate, and the pH of their blood all rise within the first minute, but by about the second or third minute their blood-pressure has begun to fall rapidly, and respiration may cease. Resuscitation by supplying oxygen is generally possible while the systolic blood-pressure remains above 100 mm. Hg, even if all respiration has ceased, but the rate of fall is rapid and the difference between success and failure may be a matter of 15–20 seconds. The pH of the blood falls as death approaches, but remains within normal limits, and is usually not far from its initial level at the end. When puppies are deprived of oxygen, their blood-pressure, respiration-rate, and blood pH do not rise but all fall progressively. Gasps may be taken for 16–20 minutes and the circulation maintained at a very low level for twice this time. Puppies have been resuscitated 26 minutes after acute deprivation of oxygen when their blood-pressure had fallen to 5·2/3·7 mm. Hg and the pH of their blood to 6·5 (Swann 1953; Swann & Brucer, 1949; Swann *et al.*, 1953, 1954). Successful survival, however, and a useful life thereafter seem to depend on the ability of the newborn animal to make use of the energy derived from anaerobic glycolysis to synthesise the high-energy phosphate bonds which are required to maintain the proper structure and function of its brain (Stone *et al.*, 1941; Himwich, 1953; Čapek *et al.*, 1956). As might have been anticipated, this resistance to oxygen-deprivation has been shown to vary with the species and the maturity of the animal at birth, but particularly with the state of development of the brain at this time. Guinea-pigs, for example, which are highly developed at birth, succumb much more quickly than rats in

a reduced supply of oxygen (Fazekas *et al.*, 1941), and the brain seems to be the most vulnerable organ, even in the undeveloped rat (Adolph, 1948; Čapek *et al.*, 1956).

A change-over from aerobic to anaerobic metabolism has two important consequences. In the first place, anaerobic metabolism produces less heat. This makes no difference to the body-temperature of a poikilotherm such as the newborn rat, but it tends to lower the body-temperature of others (unless they are in very warm surroundings), particularly of those with imperfect control of their body-temperature. Secondly, it calls for the rapid breakdown of body-glycogen and leads to the accumulation of acid end-products. A fall in body-temperature slows down all the chemical processes of the body—including the breakdown of glycogen and hence the accumulation of acid metabolites, either of which may be fatal. Many experiments have demonstrated the survival-value of this fall in body-temperature. Thus Fazekas *et al.* (1941) and Himwich (1953) found that the survival-time of day-old rats in nitrogen was raised from 20 minutes to 50 minutes by lowering their body-temperature from 34°C. to 24°C. (see also Adolph, 1948). More recent and more extensive experiments on newborn guinea-pigs have shown that cooling the animals in icewater up to the neck prolongs their life when they are made to breathe a mixture of 95 per cent nitrogen and 5 per cent carbon dioxide (Miller & Miller, 1953; Miller 1954; Miller *et al.*, 1954).

A reduction in the partial pressure of oxygen in respired air has been a common enough human experience since men began to mountaineer, and the effects in adults have been well investigated. It is generally recognised that there is no reduction in oxygen-consumption when the pressure of oxygen in the ambient air falls, even to the low levels met with at very high altitudes (Houston & Riley, 1947; Pugh, 1957). The oxygen-tension falls in the arterial blood, but a sustained increase in respiration and alveolar ventilation helps to maintain the supply of oxygen to the tissues. This is true also of the adult dog (Cordier & Mayer, 1935; Gorlin & Lewis, 1954) and to a somewhat lesser extent of the rabbit (Hamon *et al.*, 1935), and no doubt of most other adult mammals. The smaller mammals, however, do not react in this way (Gellhorn & Janus, 1936), and the oxygen-consumption and body-temperature of mice begin to fall when the percentage of oxygen in the surrounding air is reduced to about 16 per cent (Chevillard & Mayer, 1935). The fall in body-temperature so diminishes the demands of the tissues for metabolic exchange that it greatly prolongs the survival-time of these animals (Strughold, 1954), and this has repeatedly been demonstrated experimentally (Campbell, 1936, 1938). It is possible that the thyroid is involved in this fall in temperature (Smith *et al.*, 1946–8). The effects of anoxia on the brain can be mitigated by an adequate supply of circulating glucose (Gellhorn & Kessler, 1942).

The human infant behaves like the adult rodents. If the oxygen in the ambient air is reduced from the normal 21 per cent to 15 per cent, there is only a trifling increase in ventilation-rate, and the consumption of oxygen falls by some 17 per cent (Cross *et al.*, 1955). Something of the same kind happens in puppies and kittens (Moore, 1956*a*, *b*). Lambs are much more mature than puppies or kittens at birth, but their consumption of oxygen also falls when the oxygen-saturation of their arterial blood falls below 50 per cent (Acheson *et al.*, 1957; Dawes, 1957). As might be expected, this fall in the consumption of oxygen leads to a fall in the rate of metabolism and body-temperature (Brodie *et al.*, 1957).

If the survival studies on adult rodents can be transferred to the human infant, they have important implications. The fall in body-temperature which accompanies anoxaemia should be regarded as making for survival rather than the reverse, provided the baby can be successfully brought back to normal, and, for this, physiological principles suggest that a supply of glucose and the oxygenation of the tissues should precede the warming of the body.

Food, Growth and Renal Function

The kidney has repeatedly been cited in the past 15 years as a weak point in the functional make-up of the newborn animal (McCance, 1950). It is perfectly true that, by suitable tests, the renal function of the newborn and very young animal can be shown to be less capable of maintaining the stability of the internal environment than that of an adult of the same species (McCance & Widdowson, 1957). The rat is a particularly good example of this, for its kidney appears to be almost functionless as a homoeostatic organ. Yet the composition and volume of the extracellular system remains within normal limits in all healthy newborn animals.

Table II

The Nitrogen Balances of Newborn Piglets which were 'Fed' or 'Not Fed'

Nitrogen (mg. per kg. per 24 hr.)	Animals given	
	Milk or milk mixtures	Water
Intake	3500	0
Output	350	250
Balance	+3150	−250

Few have realised the importance of this discrepancy between experience and experiment, but we have been worried about it for 10 years or more. If the kidney of the newborn really is so ineffective, how is homoeostasis maintained ? We began to search for a second mechanism which we shall now describe.

If an animal is growing, some of the material in its food is always being incorporated into its tissues and does not, therefore, present itself for excretion by the kidney. This relieves the kidney of the newborn animal of much of the work which it is called upon to do in adult life. The overwhelming importance of growth in relationship to every function of the body was recognised by Edwards (1824): 'Dans la jeunesse tout paraît tendre au développement et à l'accroissement du corps.' It was emphasised by Stransky & Bálint (1920) as an aspect of renal function but facts of this kind are often not appreciated till they have been demonstrated experimentally. This we have been able to do (McCance & Widdowson, 1956) (Table II). Nine-tenths of the protein nitrogen in the food of a newborn piglet is incorporated into its tissue and never presents itself to the kidney for excretion as urea. The same is true to a lesser extent of the human baby. 'Weak' and immature, therefore, as the kidney of the newborn may appear to be when subjected to some such test as the urea clearance or the excretion of para-amino-hippuric acid, it is fully capable of maintaining the blood-urea and creatinine within normal limits, provided growth is taking place as it should. Homoeostasis in the newborn animal is maintained quite as much by its capacity for growth as by its kidneys, lungs, and other integrated organs.

The capacity for growth can be saturated only by an optimum diet, and the percentage of protein, fat, and carbohydrate in the mother's milk has long been known to be correlated with the growth-requirements of the newborn animal (Bunge, 1898). It now seems that the inorganic constituents of the diet must also be correlated with the function of the kidney and growth. The amount of calcium and phosphorus in human milk, for example, would never support the bone growth of a healthy piglet. The kidney of the newborn animal has a lower sodium-clearance than that of its mother, and a rise in the concentration of sodium chloride

in the diet may not be followed by a correspondingly large rise in the rate of excretion. The piglet and the human baby are very alike in this respect. Salt may be retained in greater measure than water and, as already mentioned, lead to a rise in the concentration of sodium in the extracellular fluids and an expansion in their volume (McCance & Widdowson, 1957). This breakdown in homoeostasis is well tolerated by the newborn animal, and may even lead to a fall in the katabolism of protein; but it is unphysiological, and real well-being can be restored only by a return to a more physiological diet.

Conclusion

The weakness and helplessness of the newborn animal has been a constant theme with philosophers and thinkers since the world began, but how true is this? The newborn infant is a good risk on the operating-table. If one can detach one's thinking from the adult, a study of the newborn in its natural surroundings suggests that many of the signs of weakness are really marks of strength—if by strength is meant the ability to survive. In the face of cold and lack of oxygen, the instability of the internal environment may enhance the newborn's expectation of life rather than jeopardise it, but a young animal cannot stage its own 'come-back'; it must be brought back. The piglet resists infections satisfactorily—if it has access to its mother's colostrum. The newborn, therefore, should be regarded as strong, provided it is left within its natural environment. It may be equally strong outside its normal environment, but only if all its physiological requirements are being met. They may, however, be met in unusual ways. Piglets a few days old will eat dry food, drink water, and grow as well in a wire cage as they do in a sty on mother's milk—but they must be kept warm (Haslett, 1957). Finally homoeostasis may depend on functions which have no place in adult life, but this need present no difficulty provided food, growth, and renal function are physiologically integrated. 'Let the weak say, I am strong' (*Joel* III, 10).

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THE NUTRITION OF THE YOUNG PIG

By I. A. M. Lucas and G. A. Lodge

The usual method of rearing piglets in the United Kingdom is to wean them from the sow at eight weeks of age but to provide them with solid food for some time beforehand, either by allowing them to scavenge from the sow's trough or, more generally, by providing them with a special food to which the sow has no access.

Within the last few years, however, the practice has developed of weaning piglets at earlier ages, anything from two days after birth or even earlier under laboratory conditions, and providing them with diets which are complete substitutes for sow's milk.

THE NUTRITION OF THE SUCKLED PIGLET

Nature of the Diet

The average piglet consumes about 2·0 lb. of milk per day, but there is considerable variation between piglets and over the course of lactation. Daily consumption recorded at the Rowett Institute rose from about 1·7 lb. per day during

the first week to 2·4 lb. in the third week, and then declined to about 1·5 lb. by the middle of the eighth week. Size of litter has little effect on daily milk consumption *per piglet* except in litters above ten or below five in number.

The conversion efficiency of sow's milk is about 0·8 lb. of milk dry matter per 1 lb. of live-weight gain. This indicates a high percentage of essential nutrients in readily available form. Composition varies with stage of lactation, and in colostrum the protein content is much higher and lactose, fat and ash contents lower than in normal milk. In normal milk, which is produced after about five days, protein and ash contents tend to rise throughout lactation while fat and lactose contents tend to fall.

Composition trends during the course of lactation observed at the Rowett Institute are shown in Table I.

TABLE I

Composition of Sow's Milk during the course of Lactation

(Means of 24 lactations recorded at the Rowett Research Institute)

	Week of Lactation								
	1	2	3	4	5	6	7	8	Mean
Total solids (%) .	19·9	19·5	20·8	20·1	20·4	19·8	19·7	19·8	20·0
Crude protein (%)	5·5	5·0	5·3	5·4	5·7	5·9	6·2	6·6	5·7
Lactose (%) .	4·9	5·0	4·9	4·8	4·7	4·6	4·6	4·4	4·7
Fat (%) . .	9·0	8·6	9·7	8·9	8·8	8·2	7·9	7·7	8·6
Ash (%) . .	0·77	0·74	0·79	0·85	0·92	0·97	1·01	1·05	0·89

Average daily crude protein intake per piglet rose from 42·2 g. during the first week to 58·0 g. in the third week and thereafter remained steady until it fell to 46·7 g. in the seventh week. The protein fraction of sow's milk contains less casein and more albumin and globulin than does that of the cow and has been found to have a lower biological value for young rats.

The content of sow's milk fluctuates greatly from day to day but varies little during the course of milking. Mean fat value determined at the Rowett Institute was 43 per cent of the milk dry matter.

TABLE II

Determinations of the Vitamin Contents of Sow's Milk. (Various authorities)

Vitamin		Highest value	Lowest value
A	mg./100 ml.	0·044	0·024
Thiamine	,,	0·098	0·063
Riboflavin	,,	0·250	0·046
Niacin	,,	0·835	0·643
Pantothenic acid	,,	0·870	0·340
Folic acid	,,	0·039	
Pyridoxine	μg./100 ml.	20·0	
Biotin	,,	1·4	
B_{12}	,,	0·167	0·105
C	mg./100 ml.	13·0	11·0
D	I.U./100 ml.	12·47	4·49

The ash comprises about 4·5 per cent of the milk dry matter, and more than half of this is calcium and phosphorus. The Ca: P ratio changes from 1: 1·5 or 1 : 2 at parturition to 1 : 0·6 in normal milk. The iron content of sow's milk is inadequate for the suckling piglet and cannot be increased by supplying additional iron to the sow.

The contents of vitamins A and the B complex in sow's milk vary with the amounts consumed, the vitamin D content is similar to that of cow's milk, and the vitamin C content is very much higher. Determined values are shown in Table II.

The mean calculated gross energy value of sow's milk determined at the Rowett Institute was 3,000 Cal. per lb. of dry matter, and this may be assumed to be equivalent to 2,750 Cal. digestible energy per lb. dry matter.

Adequacy of the Diet

Nutriments provided by the average sow are insufficient to maintain the initial rate of growth of 0·5 lb. per piglet per day beyond the first three to four weeks. To achieve a weaning weight of 40 lb. at eight weeks it is necessary for the piglet to consume about 30 lb. of supplementary food having a digestible energy value of about 1,400 Cal./lb., a crude protein content of about 17 per cent, Ca and P contents of 0·8 per cent and 0·5 per cent respectively, and containing 0·5 mg. vitamin A and 90 i.u. vitamin D per lb.

Nutrition of the Early-weaned Piglet

Weaning at Birth

This has been successful under strictly controlled laboratory conditions, but elaborate precautions are necessary when piglets are weaned without colostrum.

Weaning at Two Days of Age

Largely synthetic diets fed in a liquid state are required and results obtained have been very variable. Very young piglets appear to be unable to utilise starch or sucrose, or protein from any source other than milk.

Weaning at Ten Days of Age or Later

Dry meal diets of a semi-synthetic nature are generally employed. Piglets of this age are able to utilise starch and all the sugars, but the ability to utilise lactose declines after about three weeks.

The required fat level in the diet is uncertain, but the optimum is probably about 8 per cent. Apparent digestion coefficients for different fats included as 20 per cent of the diet have been determined, and of those examined butterfat had the highest digestibility, followed by lard.

Many estimations of protein requirements of piglets have been published, but the optimum would appear to be about 28 per cent of the diet up to 25 lb. live weight and 18 per cent thereafter. Differences between estimates of requirements are caused mainly by large variations in the efficiencies with which the different proteins are utilised. Efficiencies decrease in the order: sow's milk protein; casein or protein from dried cow's milk; casein or dried cow's milk protein plus fish-meal or soya-bean protein, plus cereal proteins.

Amino-acid requirements have been determined for several of those known to be essential. The methods of determination employed have all had disadvantages, and the results obtained, where there has been duplication, have been variable.

Little is known of the specific mineral requirements of young pigs and successful diets have contained complex mineral mixtures containing all the elements believed to be essential. More precise data on mineral requirements are available only for pigs of over 30 lb. live weight reared by the sow.

Vitamin requirements of pigs of one weight-range vary with individuality of the pig, housing, climate, bacterial synthesis in the gut, the balance of other nutrients in the diet, and the feeding of antibiotics. Consequently stated minimum requirements can be only guides to actual requirements. Best estimates of vitamin requirements are given in Table III.

TABLE III

Estimations of Minimum Vitamin Requirements for Young Pigs

Vitamin	Pigs live weight		
	10	25	40
A (mg./lb dry matter)	0·16	0·13	0·13
Thiamine. (mg./lb. dry matter)	0·57	—	0·48
Niacin. (mg./lb. dry matter)	8·0	—	7·2
Riboflavin. (mg./lb. dry matter)	1·0	—	0·65
Pantothenic acid (mg./lb. dry matter)	5·1	—	4·5
Pyridoxine (mg./lb. dry matter)	1·0	—	0·95
B_{12} (μg./lb. dry matter)	6·8	—	4·8
D (I.u./lb. dry matter)	120	100	100

Antibiotics have been universally included in early weaning diets in amounts ranging from 7 to 112 mg. per lb. of meal. While higher levels generally have been found to produce better results than lower levels, an optimum level has not been decided. Of other growth-stimulants which have been tried, viz. surfactants, sulpha drugs and arsenicals, only arsenicals have been reported as producing significant responses when included at a level of 90 mg. per kg. of dry matter in the diet.

THE NUTRITION OF THE EARLY WEANED DAIRY CALF

By Dr. J. H. B. Roy

NUTRITION OF THE PRE-RUMINANT CALF

Unlike the human infant, the newborn calf receives all its antibodies through ingestion of colostrum. Without colostrum, calves will frequently die from an *Escherichia coli* septicaemia; and even if calves are given colostrum and exposed to a heavy infection of certain coliform strains, they may succumb at a later age from dehydration owing to scouring brought about by a localized intestinal infection of *E. coli*. Some of these strains of coli are antigenically the same as those recovered from cases of infantile diarrhoea. Certain antibiotics, in particular the tetracyclines, will give protection against these conditions.

Colostrum is also a rich source of carotenoids and vitamins, particularly the fat-soluble ones, whose concentration is much higher than in normal milk. The calf is born with low liver reserves of these vitamins and this deficiency is made good by ingestion of colostrum. The concentration of these fat-soluble vitamins in colostrum is, however, affected by the feeding of the dam during pregnancy.

After the colostrum-feeding period of about four days, calves are usually fed on whole milk for at least the first three weeks of life and thereafter on a milk substitute. During the pre-ruminant period the calf requires about 135–145 Cal./$kg^{0·73}$/24 hr. for maintenance and a further 1,050–1,250 Cal./day for a gain in weight of 1 lb./day.

Milk substitutes fed directly after the colostrum-feeding period have in general given less consistently satisfactory results than whole milk. Most substitutes are based largely on the by-products of the milk manufacturing industry, although some contain cereal products. Recently it has been shown that the pre-ruminant calf cannot digest starch or the degradation products dextrin and maltose. Of the

carbohydrates tested, which included sucrose, only glucose and lactose appeared to be of use. As it is known that diarrhoea and unthriftiness are associated with intakes of over 250 g. sugar daily, it is unlikely that soluble carbohydrates can form the main source of energy during the early post-natal period, and moreover it has been suggested that fat is essential for the young calf. The requirement of fat is probably quite low for it is possible to rear calves on a skim-milk diet supplemented with fat-soluble vitamins after the colostrum-feeding period. Of the milk by-products it seems probable that only buttermilk has a sufficiently high content of fat to give practically normal growth without the addition of extra fat.

The addition of fat to reconstituted dried skim-milk is beyond the resources of the farmer, for unless correctly emulsified and homogenised, such diets cause profuse diarrhoea and loss of hair. The selection of fat for inclusion in such diets must also be done with care, for difficulty has been experienced with the use of fats containing a high proportion of unsaturated fatty acids. However, it has been shown that the variation in apparent digestibility of different fats can be largely accounted for by the chain length of the constituent fatty acids rather than by their saturation. Thus, the shorter the fatty acid chain, the greater the digestibility. Nevertheless, the feeding of highly unsaturated fatty acids is associated with the condition of muscular dystrophy.

No suitable substitute for milk protein in the diet of the pre-ruminant calf has yet been found. Moreover, even dried skim-milk processed at a high preheating temperature may be of less value to the young calf than fresh skim-milk or dried skim-milk processed at a lower temperature. This difference shows up particularly under conditions of high 'infection' with *E. coli* and may be the result of denaturation of some of the soluble proteins by heat treatment. Moreover, such milks do not clot with rennet without the addition of Ca ions.

About 26 per cent of the calories in whole milk are derived from protein, but the requirement of the calf is much lower than this, especially at low weight gains. When sufficient energy is given to cover the maintenance requirement of the calf, as little as 7 per cent of the calories are necessary as protein, whereas for a gain of 2·2 lb. the value is about 22 per cent. On low levels of milk feeding, the limiting factor for calf growth is, therefore, a shortage of energy rather than of protein.

Nutrition of the Ruminant Calf

The age at which transition to the ruminant method of digestion occurs is to a large extent dependent on the diet that a calf receives. The longer the period that a calf has access to a plentiful supply of milk, the less will be its urge to supplement its diet with other foods. Given a limited quantity of milk, the calf will eat alternative foods at a very early age providing they are palatable. Owing to the difficulties of formulating milk substitutes, the present trend is to exploit, at the earliest age possible, the calf's instinctive desire to become a ruminant, with the many advantages that accrue. The microbiological activity in the rumen makes it possible for the young calf to obtain its energy from fibrous and starchy foods, to synthesise B vitamins and to synthesise protein material from non-protein nitrogen. Moreover, once the rumen begins to function, the incidence of scouring is negligible.

Although roughage ingestion increases the volume of the reticulo-rumen, the development of the rumen papillae is related to concentrate feeding. A proportion of hay must be included in the ration of young calves, not only from the viewpoint of normal rumen function, but also for the early development of an adult-type rumen microbial population. Workers in America have shown that when the proportion of grain to hay in the ration exceeded 3 : 1 types of bacteria associated with the digestion of hay disappeared. They suggested the need for rumen inoculation with the cud of an adult animal to ensure a normal microbial population, but this has not been confirmed by other experiments.

The nervous mechanism controlling the various muscular phenomena of rumination is very active in the two-week-old calf and slight stimulation such as the presence of recording balloons often produces strong and frequent regurgitation efforts.

Of dry foods for the young calf, grass is by far the cheapest and can form the sole diet from at least eight weeks of age providing a weight gain of the order of 1·3 lb./day is all that is required. Unfortunately, the majority of calves are born in this country during the winter months, when grass is not available. With other dry foods, most consistently good results have been obtained with weaning at eight weeks, but recently quite good results with calves weaned at thirty days of age or even abruptly at three weeks of age have been achieved.

In making full use of the rumen at an early age, with its capacity for digesting cheap foods, the lower digestibility of such foods compared to that of milk, and the high heat increment and consequent low net availability of metabolisable energy of foods digested in the rumen must be put on the debit side.

The percentage of protein necessary in dry foods has not yet been firmly established. As growth in the early stages on dry food is not likely to be very fast, it is probable that the protein percentage need not approach that of whole milk. Satisfactory results have been obtained with a 16 per cent protein mixture. Because of the ability of the rumen microflora to synthesise the B vitamins associated with animal protein, there appears to be no advantage in the use of animal rather than vegetable protein.

Palatability of the dry food is necessary for ensuring maximum consumption; in particular the sweetness of the ingredients seems to be important. Pelleting of the dry food has been shown to increase palatability, and it is generally considered that young calves prefer whole or coarsely-ground cereals to more finely-ground meals.

Conclusion

With all artificial rearing systems, weight gains during the early period after birth will tend to be lower than with suckling, unless uneconomically large quantities of milk are fed. With liberal feeding after the rumen is fully functional, much of this lost ground can be recovered. The difference in cost between the energy in whole milk and in oats, hay, grass silage and high-protein cake is such that the initiation of early rumen function is essential if rearing costs are to be kept down.

ANIMAL HEALTH IN RELATION TO BRITAIN'S FOOD SUPPLIES[1]

by

J. N. RITCHIE, C.B.

THE HEALTH of farm livestock obviously has an important effect on the food supply of Great Britain. This does not arise only because of the direct loss of farm animals through deaths from disease but also from the failure of unhealthy animals to produce at their optimum potential. Further, the extent to which we are more or less self-supporting in any particular product will influence importations.

In the first place, it is necessary to ensure that herds and flocks are maintained free of the major epidemic diseases or that those diseases are kept under adequate control. Fortunately most of these diseases have been eradicated from the country, although it is still necessary to guard against their re-introduction. We are subject to periodic invasions of foot-and-mouth disease; and swine fever and fowl pest are still problems which test our control measures.

IMPORTATION

Of all meat—beef, mutton, pig meat—home production accounted for 47 per cent in 1938 and 62 per cent in 1954, while it accounted for 83 per cent of poultry meat in 1938 and 77 per cent in 1954. Imports of animals and their products must be strictly controlled in order to prevent the introduction of animal diseases. Livestock imports into Great Britain are strictly controlled and come in unrestricted quantities only from areas which enjoy freedom from the major epidemic diseases (Ireland, the Channel Islands, the Isle of Man). From other sources it is only in exceptional circumstances, and under quarantine measures carefully devised to cope with those diseases peculiar to the exporting country in question, that farm animals are accepted. Similarly, efforts are made to reduce the risks attaching to importation of animal products. Broadly, this is done by prohibiting the landing in Great Britain of a carcase or part of a carcase of swine, bovine, sheep, goat or other ruminating animal except under licence. To reduce licensing to a minimum and to interfere as little as possible with trade, a series of schedules is included which sets out the products and countries which are exempted conditionally or unconditionally from the prohibition. Alterations in the schedules may be made and are based on a knowledge of the disease position in the particular country. The importation of poultry, poultry meat and hatching eggs is also prohibited under similar regulations. In addition, waste food material is required to be boiled before being brought into contact with animals or poultry.

It is obvious that an importing country must have full knowledge of the disease position in those countries with which it trades in livestock and their products. Not only is it necessary to know which diseases exist but to know how disease control is exercised. A great deal is done by international organisations such as O.I.E. and F.A.O. to disseminate information and efforts are made through such organisations to ensure that international co-operation is fostered. It is not sufficient for these organisations to provide information for the purposes of setting up international safeguards against disease; they need to distribute technical information

[1] Address delivered to Section M (Agriculture) on September 6, 1957, at the Dublin Meeting of the British Association. Mr. Ritchie is Chief Veterinary Officer at the Ministry of Agriculture, Fisheries and Food.

and organise concerted action. This can only be done if countries are prepared to give full co-operation.

There are notable examples in recent years of the dangers: for example, foot-and-mouth disease was introduced to Canada, where it was previously unknown, in 1951, probably carried by an immigrant farm worker from Germany; blue tongue, a virus disease of sheep, which had been confined to South Africa until recorded in U.S.A. in 1948, although perhaps present for some years, was introduced for the first time to Europe when it reached Portugal, probably conveyed from Africa in cattle which, while showing no symptoms or very mild evidence of disease, may harbour the virus, which can be conveyed to sheep by biting insects (culicoides).

In spite of all precautions which can be taken in regard to importation and with general regulations which require the boiling of swill before it is brought into contact with animals, we have had introductions of foot-and-mouth disease which have been attributed to imported meat from South America. Of 32 primary outbreaks in 1956, for example, 17 originated in this way. Other outbreaks arose by indirect means from Europe. It is obvious, therefore, that with all the safeguards that may be set up, a highly diffusible disease may still be introduced. It is, therefore, of great interest to all countries to co-operate in the international field in an effort to ensure that good control measures are exercised in every country.

Important Epidemic Diseases

There can be no doubt that the first task of those dealing with animal diseases must be to bring these major diseases under control.

Without a good organisation providing country-wide cover and supported by sound diagnostic facilities and investigational and research teams, any system of disease control remains theoretical. The method used for any particular disease must vary with the nature of the disease, its incidence and distribution, and the practicability of control measures in the light of knowledge of the diseases.

Patently, if a practicable method of eradication can be devised and is economical it should be adopted. With animal diseases this is often possible when a similar problem would pose insurmountable difficulties to the medical profession. Farm livestock are destined for the abattoir eventually and policies which involve the slaughter of diseased or infected animals and their contacts are therefore a reality.

The United Kingdom has dealt with its outbreaks of foot-and-mouth disease by the stamping-out policy. In 1956 this involved the slaughter of approximately 10,547 cattle, 13,133 sheep, 4,813 pigs and 42 goats, for which compensation to the owners amounted to approximately £825,000, to which must be added some £250,000 for other expenses including the cost of administration. During the course of this particular year it has become more than ever evident that many factors play their part in the success of such a policy. They may be broadly enumerated as follows:

1. Early notification of a suspicion of the presence of disease.
2. A meticulous system of dealing with such reports must be in force and must be readily put into effect—the system must include rapid diagnosis—immediate control of movement of stock over an area—immediate quarantine of the suspected or infected farm—tracing of all contact animals and slaughter of direct contacts on other farms, e.g. animals recently moved off the infected place and animals handled by the owner of the infected place or his veterinary surgeon after contact with infection.
3. Rapid means of slaughter and disposal of carcases on the infected place.
4. An organisation capable of dealing with all the detailed tracing of stock which is necessary.

5. A system of recording movements of stock must be permanently in force and enforced to allow of easy tracing of animals.
6. Visits to examine stock in the vicinity of outbreaks must be made to discover secondary outbreaks as early as possible and also to discover whether the first reported case is in fact the primary one.
7. There must be considerable elasticity in financial arrangements to allow of vigorous pursuit of the policy.
8. The farming community must be willing to co-operate in every aspect of the work.

There are regular patterns of major movement of animals in Great Britain as, for instance, imported Irish cattle from ports through markets to farms; store cattle from the rearing areas to the feeding areas, many through regular or seasonal markets; extensive northward movement of calves from breeding to rearing areas. All these examples are important and there will probably always be considerable traffic in stock as a background to a flourishing and progressive agriculture. In the course of the eradication campaign there has been a great deal of added movements of cattle as herd replacements, sometimes to the extent that the whole of the adults in a particular herd would be removed because of the high incidence of reactors. This extensive movement of cattle has probably had an effect in distributing

TABLE I

Percentage of total wastage and disposals

	WITHER'S SURVEYS			SUMMARY OF SURVEYS	
	1950–2	1952–3	1953–4	1928–1931	
Infertile	17·5	15·2	12·6	Sterility and abortion	26·8
Deaths	5·6	4·6	5·6	Death and miscellaneous diseases	10·4
Disease and accident	26·8	19·4	23·3	Udder disease Accident	7·7 1·5
				Tuberculosis, Jöhne's disease and wasting	9·7
Total, death and disease	49·9 [1]	39·2	41·5		56·1
Reactors	included above	4·2	12·1	Tuberculin test	3·6
Poor yield	19·6	27·6	25·8	Low yield	17·7
Aged	8·9	8·0	5·6	Old age	4·3
Surplus	21·6	21·0	15·0	Trade	18·3
	100·0	100·0	100·0		100·0

[1] Includes reactors to tuberculin.

animals infected with other diseases and even in introducing certain diseases into areas where they were practically unknown.

In order to decide which important problems must be dealt with after the tuberculosis campaign has been completed, it is necessary to obtain much better information on the incidence and distribution of a variety of diseases. A start had been made with surveys mainly aimed at learning the methods which must be employed to obtain sufficient data. For convenience, a summary of surveys carried out by Withers from 1950 to 1954 is compared with summaries quoted by the Cattle Diseases Committee already mentioned (Table I). In the later surveys 21·9 per cent of the total cows were disposed of each year (varying from 18·3 per cent in a survey in Ayrshire, in 1930, to 26 per cent in a survey by N.I.R.D., in 1930 to 1931). In Withers' surveys in counties in southern England disposals varied from 22 per cent to 27 per cent, mainly depending on the amount of surplus sales. In the earlier surveys quoted disease accounted for 54·6 per cent of disposal, on average, and in Withers' surveys, some thirty years later, the comparable figure is 49·9 per cent,[1] 39·2 per cent and 41·5 per cent. It is notable that infertility is an important cause of disposal in each group of surveys.

Progress in Reduction of Diseases

It may be convenient to look at the situation over the last twenty years or so—a period after the diseases of animals which had been such a serious problem in the nineteenth century had been eliminated.

NOTIFIABLE DISEASES

Among the notifiable diseases (Table II) two have disappeared—parasitic mange of horses since 1948 and sheep scab since 1952. As is to be expected, there

Table II

Numbers of animals affected by notifiable diseases

	Anthrax	Foot-and-mouth disease	Mange	Scab	Swine fever	Fowl pest	Rhinitis	Tuberculosis Order
1936	468	67	111	255	1,873	–	–	23,716
1937	743	187	115	253	982	–	–	22,425
1938	830	190	46	222	951	–	–	19,910
1939	699	99	36	276	3,286	–	–	17,686
1940	564	160	19	228	5,019	–	–	15,501
1941	399	264	21	255	1,088	–	–	14,212
1942	372	670	28	283	451	–	–	13,480
1943	283	27	9	257	547	–	–	14,360
1944	189	181	8	245	1,449	–	–	11,747
1945	119	129	6	121	928	–	–	9,633
1946	95	54	7	94	347	–	–	8,266
1947	121	104	1	103	37	2,222	–	6,545
1948	118	15	1	69	27	267	–	6,320
1949	244	15	–	46	5	582	–	5,813
1950	344	20	–	26	430	172	–	5,296
1951	407	116	–	16	1,343	844	–	3,771
1952	1,215	495	–	1	891	498	–	2,831
1953	609	40	–	–	2,713	978	–	2,226
1954	350	12	–	–	1,445	795	4	1,762
1955	764	9	–	–	1,403	906	8	1,251
1956	1,245	162	–	–	741	956	11	1,103

[1] Includes animals disposed of as reactors to tuberculin.

has been a notable reduction in the number of cattle slaughtered as clinical cases of tuberculosis, a reduction from 23,716 in 1936, which was the peak figure since the Tuberculosis Order came into force in 1925, to 1,103 in 1956. The other notifiable diseases have shown considerable fluctuation; foot-and-mouth disease varying upwards from as few as 9 cases per annum and generally depending on the situation in Europe or in South America. Swine fever was as low as 5 outbreaks in 1949, after a serious upsurge during the war attributable to imported pig products from the U.S.A., but has since reverted to the earlier level of incidence. Anthrax has varied over these years from the low figure of 95 outbreaks in 1946 to the highest figure recorded of 1,245 in 1956. It is of interest to note that even with the larger number of outbreaks the number of animals affected is only slightly over one per outbreak. There is a close relationship to imported material, mainly of animal origin, such as bone meal for feeding stuffs or fertilisers. Three other diseases have been scheduled since 1936, fowl pest introduced with imported European carcases in 1947, since when large-scale outbreaks have occurred; atrophic rhinitis in pigs, first brought to notice in Landrace pigs imported from Sweden in 1954; and virus hepatitis of ducks, of which the origin is obscure, but for which a valuable vaccine has since been developed.

Vaccination has obviously succeeded in protecting stock against infection. The essentials for its success as a policy would appear to be that:

1. A systematic policy of vaccination has been decided, whether it be by annual vaccination, as in the Netherlands, or by the methods used in Belgium and Denmark, or by 'frontier' vaccination or 'ring' vaccination.
2. Sufficient supplies of trustworthy vaccine are available.
3. Staff is available capable of organising and carrying out vaccination of the animals which the particular policy requires to be vaccinated.

Both the stamping-out policy and vaccination policy have been successful where they are appropriate and systematically and efficiently pursued. The number of outbreaks in the Netherlands gives ample proof of the efficacy of vaccination and while there has been a number of outbreaks in the German Federal Republic and Belgium, they are far less than have been experienced during earlier epidemics and the weight of infection on infected places is much lighter because it has usually been found that only unvaccinated young cattle and pigs become infected. In consequence, the danger to neighbouring and other countries is markedly reduced, *cf.* the minor invasion of Denmark from the German Federal Republic.

The stamping-out policy can only be applied in somewhat extraordinary circumstances, and under a somewhat specialised organisation, and where funds are made available to allow of its vigorous (almost ruthless) application. These conditions do not exist in many countries. It is patently impossible to make the bold change in one step—from unorganised vaccination to a stamping-out policy, with its detailed organisation. Other preparatory phases must intervene and the preparation, in the light of experience, should obviously be by the introduction of a really efficient policy of vaccination in the first place. A stamping-out policy to supplement vaccination is of such obvious value—by reducing the weight of infection arising from the establishment of disease among the few unprotected animals—that it might well also be an early aim. However, this cannot be applied until the system of vaccination is efficient enough to reduce the numbers to be slaughtered to a reasonable figure likely to be acceptable economically and by the farming community. The phases might therefore be summarised:

1. An agreed vaccination policy, systematically carried out.
2. A combination of slaughter with vaccination.

3. A reduction in routine vaccination and a change to a slaughter policy supplemented by tactical vaccination (this is only possible in a country if all neighbours and countries from which imports, etc., are made have reached phase (2)).
4. A complete stamping-out policy (this is only possible when all countries in a region have reached phase (3)).

Similarly, a stamping-out policy has been adopted in regard to fowl pest. It is much more difficult to ensure that the traffic in poultry and all their products is properly brought under restrictions than it is with the larger farm animals, but the slaughter policy gives the only prospect of eradication. Compensation for birds slaughtered, hatching eggs destroyed and for measures of disinfection represents an approximate annual cost of £600,000 since 1947. It has been estimated that if the disease was uncontrolled and 10 per cent of flocks became affected losses from this disease might reach a figure of £3,600,000 per annum, embracing loss through deaths, reduction in eggs produced and reduced food conversion; and with a system of control by vaccination, with an estimated loss to the extent that it falls short of full protection, the costs would range between £770,000 and £1,850,000.

On the other hand, in Great Britain swine fever is virtually endemic. In this instance the use of movement control measures, the control of markets and voluntary vaccination of pig herds has been accepted in contradistinction to the situation in such countries as Ireland and Canada, where a policy of slaughter is practicable.

OTHER DISEASES

With less spectacular diseases it is much more important to acquire knowledge of the incidence and effect of the various diseases for the purpose of deciding whether and how they should be attacked—by immediate efforts at elimination where appropriate measures can be taken, by official schemes of control, by publicity of methods of treatment or control, or as a long-term aim by the encouragement of researches to provide a means of control.

A Committee of the Economic Advisory Council reported on cattle diseases in 1934 and the report is virtually an assessment of the situation along these lines.

The diseases which were then considered to be of greatest importance were tuberculosis, contagious abortion, mastitis and Jöhne's disease. Mention was also made of the serious losses arising from infertility.

As a result of this Committee's work schemes for the eradication of bovine tuberculosis have been evolved and elimination of bovine tuberculosis from the herds of Great Britain is likely to be achieved in 1961. The development of a satisfactory vaccine has brought contagious abortion under control and the advent of new therapeutic substances has had a favourable influence on the control of mastitis. Jöhne's disease still remains a serious problem not, indeed, much nearer practical solution than it was in 1934 when the Committee reported that 'Jöhne's disease cannot yet be identified with any certainty before clinical symptoms appear, and concerted steps to eradicate it must await further research'.

It is evident that infertility is still a burden on the industry despite the use of S.19 vaccine against contagious abortion. This vaccine has certainly reduced the incidence of abortions from this cause. However, other infectious forms of infertility have come to light, possibly as a result of the reduction in contagious abortion. One of them, trichomoniasis, is seldom encountered nowadays because in those parts of the country where it was troublesome it was quickly brought under good control by the use of artificial insemination. Artificial insemination, now practised to the extent that more than half the breeding females in England and Wales are mated by this method, provides excellent means of control of venereal diseases, provided the health of the bull is assured. Further, an opportunity

arises for closer study of other causes of infertility in the female because the health status and fertility level of the bulls at A.I. centres is known.

With the successful eradication campaigns against tuberculosis it has been demonstrated in several countries that an insidious disease may be eliminated by painstaking effort over many years, provided the scheme is soundly based on a knowledge of the disease and has the support of the farming community. This campaign in Great Britain has illustrated the need for all the facilities mentioned, for it has been a team job. Veterinary surgeons in practice have been employed on a part-time basis to carry out tuberculin tests and in consequence have become available to farmers throughout the country, even in remoter parts; an organisation of veterinary staff fully employed on official work has been deployed over the whole country, and has been available for any emergency work that has arisen; research workers have developed more reliable tuberculins, uniform in biological activity between successive batches, and administrators have ensured a programme of work exploiting success in localities to build areas of freedom from infection, gradually progressing in an orderly way until the whole country is embraced.

It is encouraging to realise that the organisation which the tuberculosis eradication campaign required has been provided and is available to deal with other problems which may require to be tackled. One of the important features is the employment of veterinary surgeons in practice and their co-operation in official schemes generally, for they are obviously the first line of defence against disease and are now well distributed over the country.

In the broad assessment of animal health, notifiable diseases are not such a serious problem to farming as they formerly were, but to deal effectively with them a considerable proportion of veterinary manpower is required and is diverted from more progressive work.

DISEASES COVERED BY SCHEMES OF ERADICATION AND CONTROL

The Tuberculosis Attested Herds Scheme and the *Area Eradication Plan* have resulted in 71 per cent of all the cattle in Great Britain being included in Attested Herds at June 1957 (90 per cent in Wales, 89 per cent in Scotland, 64 per cent in England). The incidence of reactors in these herds is under 0·3 per cent of animals tested and in the longer-established attested areas it is as low as 0·1 per cent. Generally, owners of herds free of tuberculosis are much more inclined to approach their problem on a herd basis and to make every effort to ensure the general good health of their cattle; for instance, he usually has his calves vaccinated against contagious abortion and takes opportunities for selection within the herd and gradually to raise his standard of production. (The national average production per cow has risen from 540 gallons in 1936 to 626 gallons in 1956–7.) The poorer types in dairy herds may possibly be used, where suitable, to breed some animals for beef.

In abattoirs, condemnations of cattle carcases in Great Britain were 2·35 per cent of the total carcase weight in 1943. In 1953 only 1·3 per cent was condemned as unfit for human consumption. An assessment of the causes for condemnation was made in 1946, when it was shown that 77 per cent of all condemnations were due to tuberculosis. At the end of 1944 the percentage of cattle in Attested Herds was only 7, and it has risen slowly to 19 in 1950. Since the percentage in June 1957 is 71 we can confidently expect that there is now a sizeable reduction in condemnations on account of tuberculosis. In some abattoirs tuberculosis is now rarely seen.

Among pigs the condemnations in the abattoirs have fallen from 2·34 per cent in 1943 to 1·1 per cent in 1953. The incidence of tuberculosis among pigs has been markedly reduced in parallel with the improvement in the cattle stocks.

Calfhood Vaccination Scheme against Contagious Abortion. Since this scheme was introduced in 1944 a sizeable proportion of calves has been vaccinated. At present

over 400,000 are inoculated each year—about a third of the census figures for female cattle under one year old. Before this vaccine came to be used contagious abortion was accepted as a source of 'very serious loss to dairy farmers, both directly by causing the loss of calves and the loss of milk, whether due to lessened productivity or to interference with normal lactation periods, and indirectly by causing disease of the reproductive organs and consequent sterility'. This loss has been greatly reduced: the abortion rate according to surveys which have been done from A.I. centres, and by Withers, is around 2 per cent of pregnancies—Withers' surveys give a figure of 3·2, 3·0, 3·3 and 3·1 in successive years. Causes of abortion were not investigated but he says 'it is known from collateral data that few of the recorded cases are due to brucella'. It is generally accepted that vaccination has brought the disease under a good measure of control. It is most unusual nowadays to encounter an 'abortion storm' in breeding herds. Vaccination has not necessarily reduced the infection rate to the same extent.

Swine Fever Registered Vaccinated Herds Scheme. Breeding herds of pigs are being voluntarily vaccinated as a precautionary measure against this disease.

Under the *Poultry Stock Improvement Plant in England and Wales* and the *Accredited Poultry Breeding Stations Scheme for Scotland* an increasing number of flocks are being tested for pullorum disease and are being maintained free of bacillary white diarrhoea. At the same time these flocks are maintained under a degree of supervision of their general health and freedom from other diseases. In 1942, when the rapid whole-blood method of testing was adopted, 2,752 flocks were included in the Scheme; 1,333,402 birds were submitted to test and 1·1 per cent gave positive results. In 1956 5,131 flocks were in the Scheme, 4,749,504 birds were tested and 0·12 per cent were positive. This shows that not only has the cover of this Scheme been increased but that the health situation in regard to pullorum disease has been markedly improved.

OTHER DISEASES

Over recent years considerable improvement has been effected in the weapons available to deal with infectious diseases which had not come under any legislative control. Developments of new therapeutic substances, including the sulphonamides and antibiotics, have succeeded in changing the picture in regard to such diseases as mastitis, for although the general incidence of mastitis of all kinds may not have altered markedly, methods of treatment are available, particularly for streptococcal mastitis, and the losses arising from the disease have been considerably reduced. Treatments have become available for such important conditions as foul in the foot, pneumonia, post-parturient infections and *Vibrio fetus* infection.

Research work carried out in the 1920's and early 1930's found a ready practical application to sheep diseases in the development of preventive vaccines and sera against diseases like braxy, lamb dysentery and louping-ill.

With many of the parasitic diseases in cattle and sheep, much investigational work on parasitic conditions has resulted in the development of more effective methods of treatment, and drugs for treatment and prevention. In addition it has led to a clearer understanding of the application of husbandry methods to the prevention of clinical disease.

The sheep population in the country has dropped by some 15 per cent since 1939 and yet the estimated production of mutton and lamb has almost recovered its pre-war level.

The diseases of poultry present a special problem. Intensive systems of rearing and housing are now the farmers' answer to the steady increase in labour costs, and it may well be that 70 per cent of commercial egg-laying units are housed in batteries, or deep litter, or in straw yards. When we consider poultry production for the poultry meat trade intensive methods are universal. In all these systems in

which an animal population is concentrated in a limited area the potential risk of disease is high—indeed it is true to say that the success of the enterprise depends on the control of disease.

While benefits to the industry as a whole would follow an extension of disease control under the breeding schemes to other categories of poultry flocks, there are limitations to our knowledge of some diseases, notably fowl paralysis and the leucoses. These are the great killers of poultry in their first laying year and a good deal of fundamental research needs to be done before we can offer the industry specific advice about control.

Modern chemotherapy has made available drugs which have proved of the greatest service against some bacterial infections and also against certain killing forms of parasitisism.

Disease Surveys

Surveys of the incidence and distribution of disease have been made from time to time. Some have already been mentioned. They are made usually for the purposes of assessing the relative importance of the various diseases in different species of farm animals. Some methods of survey may be quite accurate as, for instance, the method of tuberculin testing of a selection of herds in 1938. By this method a good assessment can be made provided the herds tested are a representative sample of those of the country as a whole or of a particular district. In this instance only a small proportion of herds was surveyed and, indeed, it was unnecessary to extend the survey further for it showed that even self-contained herds over the whole of Great Britain showed 13 per cent reactors. This was sufficient with a disease of high incidence to confirm that there was a heavy weight of infection and that the task of eradicating the disease was a formidable one. It is much less easy to carry out reliable surveys for disease of lower incidence and for which tests are not available. In a paper in connection with a survey of sheep diseases Heath suggested that there were six methods which might be followed: statistics of mortality provided by farmers; detailed statistics from small numbers of farms; a study of statistics available from the Ministries of Food and Agriculture; records of materials received at laboratories; collection of material from abattoirs; and collection of material from knackers. All these methods might well be used but their limitations must be appreciated and any investigations must be designed in such a way that the results are capable of proper interpretation. Surveys have already been made to assess losses among calves, pigs, and dairy herds. We need to know which diseases require particular attention, whether it be to decide that further research is necessary or to consider methods of control. It must be realised in this connection that unlike the medical profession the veterinary surgeon has no vital statistics centrally compiled with which he may compare the situation in a particular locality or in a particular class of animals.

Public Health

This paper would be incomplete without reference to the public health aspect. Time and space will not allow of more than a mention.

Bovine tuberculosis was at one time a serious hazard to man mainly through consumption of infected milk. The progress of the eradication of the disease from cattle and the extension of compulsory heat treatment of milk have combined virtually to eliminate the danger in rural and urban areas.

Other diseases which would require full discussion are brucellosis (undulant fever), salmonellosis, staphylococcal infections and parasitic conditions in which a particular stage of the parasite infests the human subject.

In a country where there is a comparatively large human population in comparison to the numbers of farm animals, and where agriculture flourishes, it is essential

to strive for a degree of self-sufficiency in a number of products. From this point of view, and also to protect against risks from imported materials, the elimination of disease and its control and the maintenance of a high level of animal health are obviously important.

Some progress has been made with some of the diseases which obviously required to be tackled first. An organisation is available with whole-time and part-time staff so deployed that it can cope with highly infectious diseases as they arise and, as has been demonstrated in connection with tuberculosis in cattle, is capable of carrying an ambitious programme of eradication of an insidious endemic disease to a successful conclusion. Inside the organisation are important elements directed towards investigation and research.

This is supported by sound teaching facilities for the training of veterinarians and the Schools are increasingly sharing in research work. Research in animal diseases is being pursued at an increased level and facilities can usually be made available when the importance of a problem or the quality of the projected programme justify expenditure on the work.

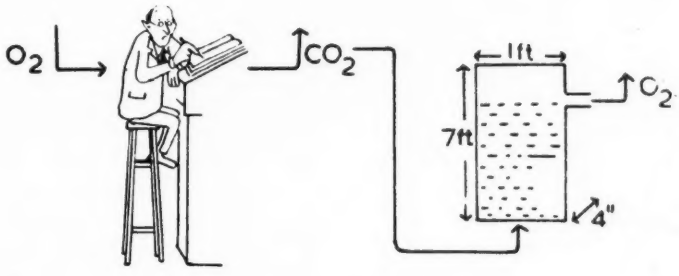
This may be accepted as showing promise that the adverse effects of animal disease in Great Britain upon food production may continue to be reduced.

THE CHEMICAL MECHANISM OF PHOTOSYNTHESIS

by

DR. C. P. WHITTINGHAM

PHOTOSYNTHESIS IS the process in which the plant utilises light-energy to convert carbon dioxide to carbohydrate with the concomitant liberation of oxygen. The net effect is opposite to that of the breathing of animals and the complementary relationship between plants and animals was first shown in the classic experiment of Joseph Priestley when he placed a mouse and a piece of mint together under a bell-jar (1). In more modern terms one may consider the possible use of algal cultures to remove carbon dioxide and supply oxygen to men enclosed in an atomic-powered submarine or a space ship. Some idea of the quantities which would be involved are shown in Fig. 1.



An amount of carbon dioxide equivalent to that produced by a sedentary man will be converted to oxygen by 16 gallons of a 1% algal suspension ($1\frac{1}{2}$ lb. wet wt algae)

PHOTOSYNTHESIS

$$CO_2 + H_2O \xrightarrow[\text{GREEN PLANT}]{\text{LIGHT ENERGY}} O_2 + \underset{CH_2O}{\text{Organic foodstuffs}}$$

Fig. 1.

Until the present century the process of photosynthesis was regarded as entirely peculiar to plants. More recently, as the nature of the mechanism has been revealed, it has become clear that the over-all process is most conveniently considered in two parts. Firstly, how does the plant trap light-energy and harness it to drive the reaction sequence in the direction of net synthesis? Secondly, what are the chemical reaction steps involved? The second question can now be answered at least in general terms and we shall see that its answer gives some clues as to the solution of the first.

The elucidation of the chemical process has been made possible by the exploitation of the modern analytical technique of paper chromatography, together with the use of the long-lived tracer C^{14}. The simplest experiment one might visualise would be to supply carbon dioxide, containing the radioactive carbon, to the plant and kill the plant immediately afterwards. If the time were sufficiently brief only one compound might be labelled, the first-formed intermediate; if a longer time

between feeding and killing were permitted one might hope to find two compounds becoming radioactive and so on, thus eventually establishing the whole reaction sequence. In fact when this experiment was tried, even within the shortest practicable exposure time to isotope (2–5 seconds), at least five compounds became radioactive to differing extents. Indeed, within only 5 minutes, radioactivity appeared in many of the components of the cell, including proteins and fats. Thus the simple type of feeding experiment had to be modified. If instead of determining whether an intermediate is merely active, the percentage activity in that compound as a fraction of the total activity fixed is measured, then by extrapolation it is possible to estimate which compound probably had 100 per cent of the radioactivity immediately after the addition of tracer. This will be the first intermediate formed

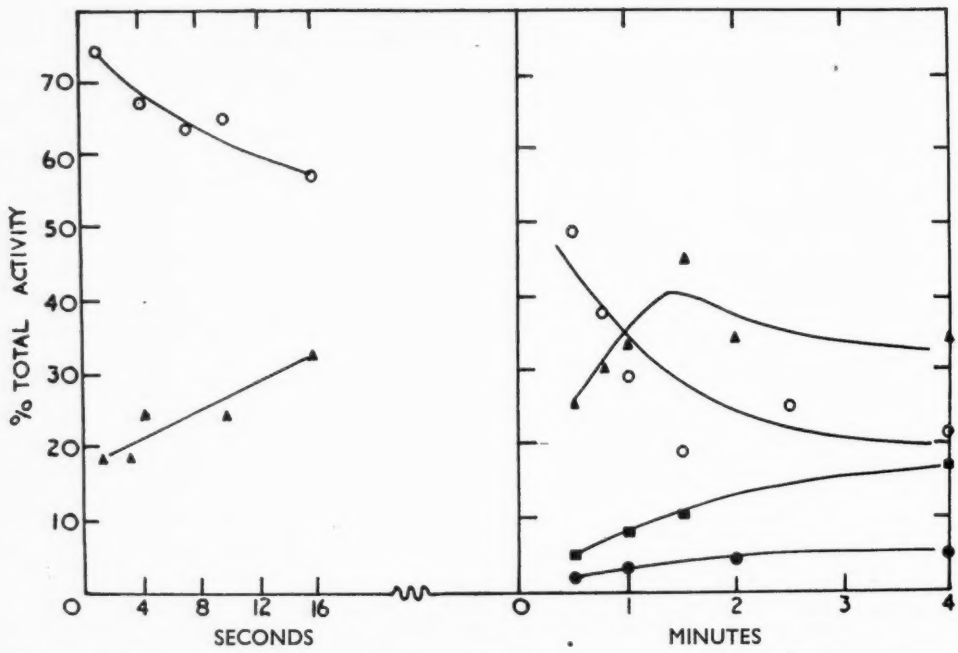


Fig. 2.—*The percentage radioactivity incorporated in different compounds as a function of time during photosynthesis in $C^{14}O_2$ for Scenedesmus. (After Calvin and collaborators.)*

○ phosphoglyceric acid ▲ sugar phosphates
■ malic and aspartic acids ● alanine

from carbon dioxide. Calvin and his colleagues (2) did such an experiment and showed that the first-formed intermediate was probably phosphoglyceric acid (PGA) (Fig. 2). Further evidence could be obtained from a different type of experiment in which the individual carbon atoms in a molecule were assayed for activity. When this was done the first-formed hexose sugar molecule was found to be labelled in the 3- and 4-carbon atoms almost exclusively. This suggested that the 6-carbon atom molecule may have been formed from two 3-carbon molecules, each having the carboxyl group labelled. Thus the first step must have been the addition of carbon dioxide to a 2-carbon molecule to give the 3-carbon molecule, phosphoglyceric acid. Some years were spent in what proved a fruitless search for this molecule until it was realised that a 5-carbon molecule would do just as well. This 5-carbon molecule, now believed to be ribose phosphate, combines with a molecule of carbon dioxide to form two molecules of phosphoglyceric acid, one containing the carbon from the carbon dioxide. To ensure that the process is maintained some of the resulting product must be fed back to re-form more 5-carbon compound, which

can then combine with more CO_2. This only takes place after the PGA has been reduced to triose phosphate, a reaction step which had been closely studied by students of respiration. Fig. 3 shows some elaboration of this bare outline of the process and by now we know a good deal of the intermediates concerned in this so-called 'photosynthetic cycle'. As often happens in research, whilst this fascinating analysis of the photosynthetic pathway was being undertaken, other biochemists, working with animal tissues on respiratory studies, were being led to formulate essentially similar reaction mechanisms. It then became clear that the processes concerned with reduction of carbon dioxide to carbohydrate, in photosynthesis, were not unique to plants. The unique feature was the ability of the plant to use light-energy to drive the reactions in the direction of net synthesis.

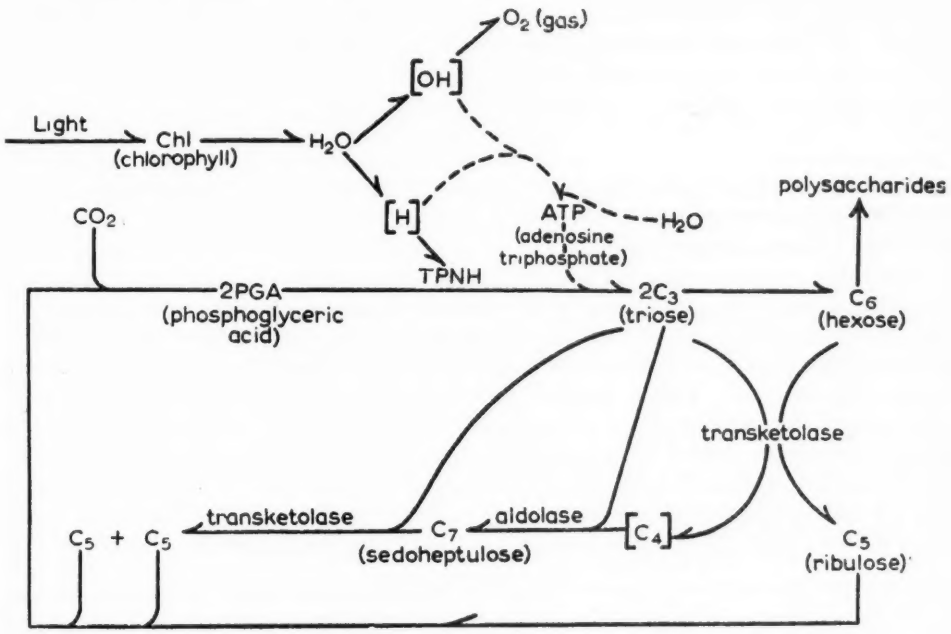


Fig. 3.—*The photosynthetic cycle* (*after Calvin*).

When we look at the cycle as described we see that for it to continue in the direction of synthesis two things must be supplied, a form of reducing power, probably in the form of reduced coenzyme, and adenosine triphosphate. Both of these must result from light absorption.

This separation of the processes of carbon-dioxide reduction, and of photochemical reaction, had been foreshadowed by the work of Dr. Robin Hill (3), at Cambridge, who had achieved a physical separation of the two processes simply by isolating chloroplasts from the plant cell. Whilst the chloroplasts, after isolation from the plant, still produced oxygen in light, they showed no reaction with carbon dioxide but required the presence of some other reagent, which was reduced during the reaction. Ferric salts could be reduced to ferrous, quinone to hydroquinone and certain dyes also. The essence of the mechanism was that, in light, oxygen was evolved from water and the hydrogen transferred along a hydrogen 'chain' to the added substance. This is shown in Fig. 4 and the general picture was consistent with similar conclusions reached by van Niel (4) on the basis of studies with the photosynthetic bacteria. The experiments of Hill and others since indicate that the essential nature of the light reaction in photosynthesis is the formation of reducing power by the 'splitting' off of 'hydrogen' from water and the removal of

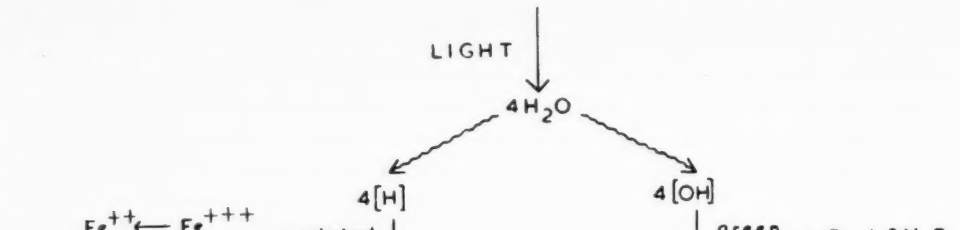


Fig. 4.—*The 'splitting' of water in photosynthesis.*
The square brackets indicate that some radical is formed containing the group in an, as yet, unknown chemical form.

the oxidised product by the liberation of oxygen. This reducing power, when in the form of a suitable carrier such as reduced coenzyme, will supply one requirement to drive the 'photosynthetic cycle'.

The other requirement, you will remember, was one of adenosine triphosphate. This substance is formed in a large variety of tissues, animal and plant, in a phosphorylative reaction which accompanies oxidation of several reduced substances. Hence it could arise by re-oxidation of part of the reduced product formed by the light reaction. This is believed to be the case except that this type of phosphorylation, originating from photochemical reaction and hence called 'photophosphorylation', differs in at least two respects from the type occurring in non-photosynthetic tissues (5). Firstly, the oxidation does not involve oxygen itself and can take place under anaerobic conditions; secondly the intermediates concerned are probably different. Fig. 5 shows a possible though speculative diagram of the

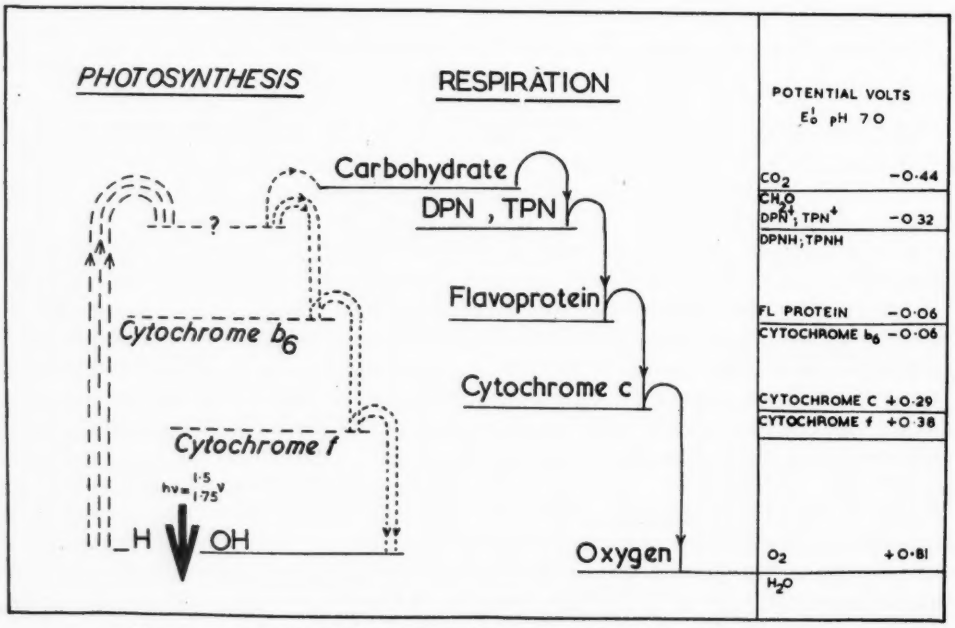


Fig. 5.—*A possible role for the cytochromes found in photosynthetic tissues.*

type of mechanism which may be involved. There are still details to be worked out here, and there is still uncertainty as to the nature of the reduced substances, formed in the chloroplast, which initiate the phosphorylative mechanism and those which result in the ultimate reduction of carbon dioxide. Furthermore, recent work indicates that when chloroplasts are isolated from the plant, with the minimum of fragmentation, they retain the ability to reduce carbon dioxide so that the theoretical separation of processes referred to earlier is not in fact a physical separation *in vivo*, at least at the gross morphological level (5).

Considering the mechanism as a whole, and in these general terms, the remaining outstanding problem is the mechanism whereby light absorption results in the production of reducing power. This activity resides in the chloroplasts and attempts are now being made to study the structure of the chloroplast, using the electron microscope. As was well known from studies with the light and fluorescence microscopes, chloroplasts are not optically homogeneous but show regions in which the pigments are relatively concentrated, the grana, amongst the less pigmented stroma regions. Studies with the electron microscope have shown both the grana and stroma to have a lamellar structure (6). What evidence is there that this structure is related to photosynthetic activity ? One type of experiment which has been done is to determine photosynthetic activity and chloroplast structure during the greening of an etiolated plant. As the plant develops chlorophyll there is a progressive development of grana and lamellae; furthermore, as the structure develops so does the photosynthetic activity (7).

Unfortunately no one has yet devised an electron microscope which will tell us what these structures represent *in vivo*. At the present time we can only speculate. Fig. 6, after Wolken (8), shows one interpretation of the lamellar structure. The

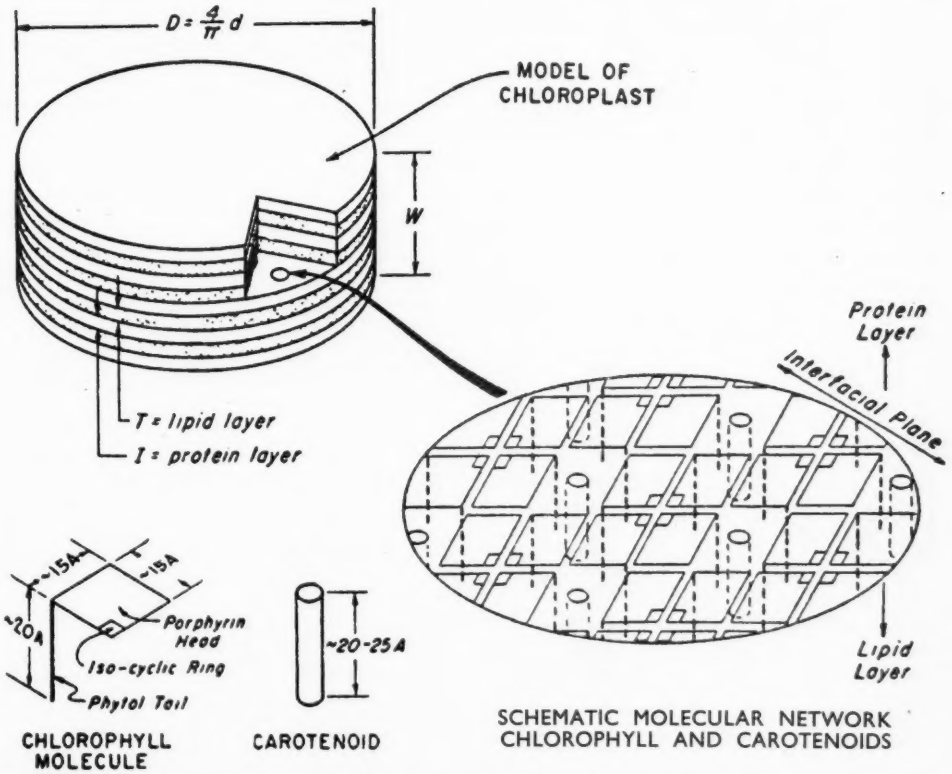


Fig. 6.—*The arrangement of chlorophyll and carotenoid pigments in monolayers in the granum, according to the suggestion of Wolken.*

proposal is that the chlorophyll molecules form a monomolecular film separating lipid from protein layers. Chlorophyll is well suited chemically to occupy this position and, further, if one calculates the average number of molecules present in the plastid, and the interlamellar surface area, one finds that the surface area of interface is of the right order to accommodate all the chlorophyll molecules. The other pigments of the chloroplast are arranged between the chlorophyll molecules.

One obvious consequence of this orderly arrangement is that the effective concentration of pigment within the granum is very high, perhaps of the order of 0·1 M.This close packing increases the probability that energy from light can be transferred from an absorbing molecule to an adjacent molecule within the very short time available before it is degraded into heat. Tentative calculations indicate that excitation energy may move from the actual molecule which absorbed the light through perhaps as many as several hundred or even one thousand molecules before it is dissipated. This transfer of energy can take place not only from chlorophyll molecule to chlorophyll molecule, but also from many of the accessory pigments also. In this way the energy absorbed by the yellow xanthophylls, and by the orange carotenoids, can be transferred to chlorophyll in some cases with very high efficiency (9). Hence the presence of the other pigments extends the range of wave-lengths of light which may be utilised by the plant, allowing some specialisation of the plant to particular environments, as for example the well-known zonation of seaweeds with the green *Chlorophyceae* in shallow waters, the red algae in deep waters, where the light is blue-greenish and the brown algae in between.

There is a further important consequence of the migration of energy through several hundred molecules. With such a mechanism it will be sufficient to supply one 'trapping centre'—at which excitation energy is converted to chemical energy and fed to the reaction path—for every few hundred chlorophyll molecules. The granum itself contains about 10^8 chlorophyll molecules so that the basic reaction unit is more likely to be some portion of the lamellar interface. The size of the basic unit can be estimated by a completely different type of experiment. If a green plant is illuminated by a very brief flash of great intensity the oxygen produced per flash, however bright the flash, never exceeds 1 molecule for every 500 chlorophyll molecules (10). The interpretation is that during the flash, which is so brief that no reaction takes place within the time of illumination, a large fraction of the chlorophyll molecules are excited. Energy is transferred to the reaction centres and since these are relatively few in number their frequency alone determines the yield per flash. It is of interest that such experiments, which were done by Emerson and Arnold as long ago as 1932, gave a value for the number of centres which is now

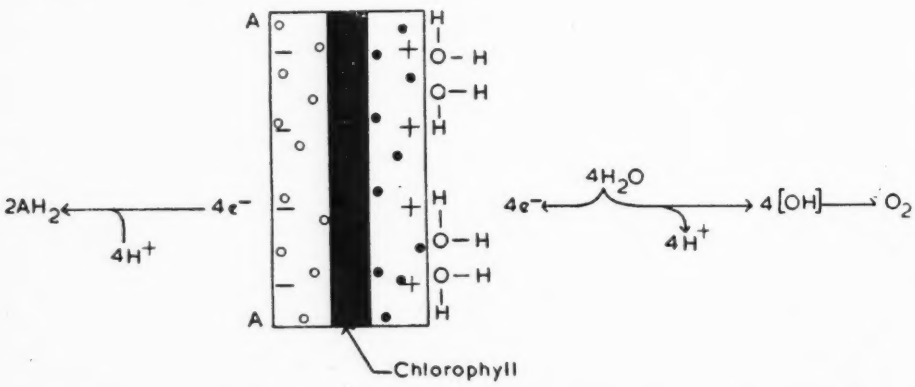


DIAGRAM OF THE SUGGESTED NATURE OF THE PHOTOCHEMICAL APPARATUS

Fig. 7.—*The polar character of the chloroplast structure as proposed by Bassham and Calvin.*

known to be in agreement with the predicted maximum permissible range for energy transfer.

Our final question must be: What happens at the trapping or energy conversion centres? Opinions still differ since there is no direct experimental evidence available. Some have proposed that there is a direct chemical linkage between certain intermediates of the carbon path and certain chlorophyll-enzymic complexes (11). Another view is that at these specific sites there is built into the chloroplast structure a polar character, such as the *p–n* junction of a transistor (12). This serves as it were to channel off electrons to one interface and positive charges to the other (Fig. 7). These then respectively react with the carbon chain and water. If this second view were proved correct the solar battery lying at the heart of each photosynthetic centre would be identical in principle to those now being developed to energise telephone lines across the American states.

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SCIENCE FOR ALL

AT the Sheffield meeting of the British Association in 1956 for the first time a collection of books for the non-specialist reader on scientific subjects was exhibited by arrangement with the National Book League. These books ranged from the history of science to forecasts of future developments and covered a wide field of the physical sciences, biology and natural history. The experiment was a success. A revised version was displayed at the Dublin meeting in 1957 and it is hoped that such an exhibition will become established as a regular event at the Association's Annual Meeting.

Now the National Book League, in consultation with officers of the Association and with experts in the various subjects, has produced a printed list of some 700 books, under the title *Science for All*.[1] Full details of each book are given, with notes on the scope of the contents and the level of comprehension required for their enjoyment. As in the parent exhibition, a substantial section on the history of science and an impressive list of general surveys are provided. There are sections dealing with method and communication, mathematics, physics, chemistry, astronomy, astronautics, meteorology and climate, geology, oceanography and marine zoology (subjects in which new techniques have recently made possible the acquisition of much new knowledge), biology, biochemistry and physiology (with subsections on genetics and evolution), zoology, botany, and, finally, technology. The social sciences and medicine are expressly excluded; the technology section covers books dealing with principles, not with 'how to do it'.

In these days of over-specialisation and rapid development, such a list serves a twofold purpose. Quoting from the book's introduction: 'The purpose of this bibliography is to provide a list of books which will help the non-specialist to understand the physical aspects of the world in which he lives, and specialists in particular fields to learn something about the activities of their fellow-workers.' It will undoubtedly also prove a useful tool for school librarians, particularly those whose duty it is to provide reading matter for sixth-form students on the arts side, and for those who wish to interest their science specialists in the historical background of their studies. The section dealing with books on 'method and communication' is of direct interest to both. *The Times Educational Supplement*, in a cordial review, stated that 'the list . . . can be given a first-class certificate for thoroughness and comprehensiveness'; we have no hesitation in endorsing this statement, and recommend *Science for All* to our members as a valuable bibliographical aid.

There is a constant flow of books in this category coming from the publishing houses, and a reading list compiled in 1957 is in danger of becoming rapidly out of date, though many of the books listed in *Science for All* have claims to a permanent position on the library shelves. The National Book League, recognising this danger, intends to issue annually a multigraphed list of selected new books, in order to keep the main work up to date. The first of these supplements will be available in the early autumn of this year.

[1] *Science for All*: an annotated reading list for the non-specialist. Cambridge University Press for the National Book League, 1958. 9*s*. 6*d*. viii, 177 pp.

NERVE STRUCTURE AND FUNCTION

SECTION D (ZOOLOGY) devoted Thursday, September 5, 1957, at the Dublin Meeting of the British Association to a symposium on the structure and functioning of the nervous system. The speakers were: Professor J. Z. Young, F.R.S., on 'The evolution of organisation within the nervous system' (Presidential Address—published in full in *The Advancement of Science*, No. 54, Sept. 1957); Dr. W. K. Taylor, 'Theories of functioning of the nervous system investigated by an electric analogue computer'; Dr. J. W. S. Pringle, M.B.E., F.R.S., 'The analysis of nerve function'; Dr. H. P. Whiting, 'Organisation of the nervous system in primitive vertebrates'; Dr. D. Vowles, 'Evolution of the insect nervous system'; M. J. Wells, 'Touch discrimination in the octopus'.

The following composite account has been prepared by M. J. Wells.

NERVE STRUCTURE AND FUNCTION

By M. J. Wells

In order to survive, an organism must detect and react in a suitable manner to changes in its environment before these become sufficiently serious to cause damage. Most animals have receptors tuned to detect small changes and separate effectors responsible for making the necessary adjustments. Some means of communication between the two is necessary. In very small animals, and in cases where adaptation need not be rapid, transmission can be achieved by diffusion of products from the receptors acting directly upon the effectors, but the speed with which information can be transmitted by this means is clearly limited and in all cases where speedy adaptation is required we find some form of nervous system, characterised by the presence of cells capable of transmitting information in the form of propagated electrical changes. The nature of these changes is remarkably constant throughout the animal kingdom; all nerve cells are alike in that they can only pass information in the form of pulses that, for any one cell, are identical in magnitude and speed of propagation. This means that the magnitude or direction of any changes detected by the sense organs can only be signalled in the form of variations in the number or frequency of nerve impulses coming from the receptors concerned, and that the effectors must be capable of translating this type of coding.

But transmission of information from receptor to effector in this way is not all that a nervous system does. We find two classes of complication. The first is that the output to the effectors is always a product of integration of inputs from a number and generally from a variety of receptors, so that the animal's response as a whole is adapted to the sum of the changes that have occurred in its environment. The second complication is that, in any case, knowing what goes into the system from the receptors very rarely permits us to predict what will pass out to the effectors. Stimulation of a receptor does not necessarily result in the same signals being passed to the effectors every time, and although such cases are known (stretch receptor—muscle responses for example) these are sufficiently exceptional to be worth noting as such. In most cases we can only hope to predict what will happen when the animal is stimulated in a particular way if we know a good deal about its past history, which implies that some trace of past events must remain within its nervous system and be taken into account when the animal responds. One of our problems is to find out how this can occur. We do not know how nerve cells store information

and we do not know what arrangements determine that this stored information is fed back into the system as required. We suppose in the absence of any evidence to the contrary that the individual nerve cells in the nerve masses where these events occur have the same properties as their peripheral dependents and that the properties of the central nervous system as a whole must depend in some way on how these units are arranged.

The internal arrangements of nervous systems have so far proved too complicated for complete maps of them to be made, and, if only because of the enormous numbers of units involved (more than 10^8 in *Octopus* and 10^{10} in man, to quote two examples given in the Presidential Address), the task may well be impossible. We must rely upon indirect methods to find out why nervous systems have the properties that they do. Either we must work out bits of such systems, searching for examples where parts that we are able to define structurally govern relatively simple integrative actions, and argue from these cases how the rest must be organised, or we must survey the broad outlines of the organisation of nervous systems in as wide a variety of animals as possible in the hope of finding principles of organisation common to them all.

Examples of both approaches were given at the Dublin meeting. In seeking simple examples of integrative action there are obvious advantages in avoiding cases where memory retention plays a conspicuous part, and it is not surprising to find that the most thoroughly worked-out examples are from those parts of nervous systems that deal with the integration of motor responses. Of these the cardiac ganglion preparation from decapod crustacea (described by Pringle) is perhaps the simplest and best understood at the present time.

The cardiac ganglion is an elongate structure lying along the dorsal surface of the heart in animals such as the lobster, *Homarus*. It is composed of five large and four rather smaller nerve cells that between them control the beating of the heart. Each of the large cells and perhaps also of the small cells sends an axon into the heart muscle; each has dendrites that ramify in the heart muscle, and each has collaterals that intermingle with similar processes from the other cells of the ganglion. The nine cells together generate a rhythmic discharge of signals to the heart muscles, causing these to contract in a co-ordinated manner. The total discharge is made up of a number (about fifty-four) of individual nerve impulses that recur in a characteristic sequence every 1·2 seconds. It can be shown by severing the connections between the cells that this pattern is a product of interactions between all the cells of the ganglion. When the cells are disconnected by drugs blocking nerve transmission, or surgically, each cell in the group is revealed as being spontaneously active and producing a characteristic steady frequency of discharge. In the intact ganglion interactions between the cells change this to a sequence of co-ordinated bursts.

Further experiments can be made on this preparation. Removal of one or more of the cells alters details of the pattern of discharge, but a 'co-ordinated discharge not qualitatively different from that of the whole ganglion may continue when over half of the cells are gone' (Maynard, 1955). Even such a limited integrating system as this shows, therefore, many features typical of much more elaborate parts of the nervous system. We find, for example, that the output is a pattern of nerve impulses distributed in space and time and that margin for safety is provided by multiple connections ensuring that loss of some of the component parts produces only minor impairment of function. We also find that the system has processes that may be assumed to bring in sensory information from the heart muscles and (in the intact animal) extrinsic nerves from other parts of the nervous system, in this case from the ventral nerve cord; the system is autonomous but provision is made for modification of its activities so that its output can be adjusted to allow for local changes in the heart muscle and for the more general needs of the organism as a whole.

Other instances where interactions between the components of comparatively small groups of cells produce a complex pattern of output to the effectors have been found in cicadas. The song of cicadas is determined by bursts of impulses passing to the muscles controlling the tympanal organ at the base of the abdomen. The nerve impulse patterns are generated in the thoracic ganglion[1] and the song produced as a result of activity in rather less than a dozen nerve fibres. In the genus *Terpnosia* a single pair determines the rhythm. This example is particularly interesting because certain species of *Terpnosia* (*T. stipata* and *T. ridens*) can be distinguished only by their song. Presumably we are dealing with a case of recent speciation as a result of variation in the connectivity of this one pair of cells—a very minor difference in the genetical control has led to a comparatively great difference in the output pattern from this part of the nervous system.

It is not entirely coincidental that both the above examples of relatively simple integrative mechanisms are from arthropods. The arthropod nervous system has certain features tending to produce decentralisation of function so that integrative systems are more likely to be found in anatomically separable parts of the nervous system in this group than in others. Vowles pointed out some of these features in his paper on the evolution of the insect nervous system. Perhaps the most important is that the nerve cell bodies themselves are not used to form connections between neurones as they are in vertebrates. In addition to this, even those cells found within the central ganglia have relatively few dendrites, so that the possibility of interaction between cells is comparatively limited. This in itself would tend to reduce the possible complexity of integrative processes. When this is considered in relation to the comparatively slow conduction rate of insect nerve fibres (of the order of 1·5 M/sec in cockroach, compared with 15 M/sec in a cold-blooded vertebrate like the frog) it can be seen why insects have tended to develop their inherited arrangement of largely autonomous segmental ganglia rather than centralised brains. A highly centralised nervous system is only of advantage in that it permits a rapid integration of sensory information from a number of different types of sense organs and a greater variety of responses to the possible combinations of stimuli; it can only do this if the cells comprising it are sufficiently numerous or can individually deal with sufficient inputs. In insects the individual neurones can deal with comparatively few inputs and the cumulative effect of long chains of slow-conducting cells would tend to produce large transient and oscillatory errors in the feed-back systems regulating fine adjustment of movement. As a result we find that insect responses, other than those arising from use of the eyes or antennae, tend to be determined at a segmental level and that in any case fine adjustment of movement is carried out as near as possible to the point of origin of the stimuli to be integrated.

It is difficult in cases like this to distinguish between cause and consequence; we do not know whether these peculiarities are a result of the limited properties of the nerve cell units themselves or the consequence of an inherited nervous organisation that would not be significantly improved if its components conducted faster or had greater possibilities of interconnection. Insects have few individual neurones, of an apparently rather inefficient type; yet insects are a very successful group and presumably derive some advantage from the very simplicity of their nervous organisation.

Whatever the advantage to the insect (a matter that is discussed later, see page 456), the advantage of the arthropod type of organisation in so far as we are concerned is that it provides parts of nervous systems that we can hope to analyse. There is no reason to suppose that groupings of cells as limited as those found in the cardiac ganglion do not determine some of the less complicated actions of vertebrates; it is

[1] The ventral nerve ganglia of cicadas are concentrated into a single mass in the thorax as in other Homoptera.

simply more difficult to locate them because the nervous systems of vertebrates are structurally so much more concentrated.

One way of overcoming this difficulty was demonstrated by Whiting. He traced the development of the system governing movement in a growing vertebrate. To simplify the problem as much as possible the animal chosen was the lamprey, a chordate whose young stages at least may be presumed to be primitive and unspecialised and therefore likely to show features of vertebrate organisation in an uncomplicated form. At hatching, the larval lamprey—a tiny animal some 4 mm. in length—has relatively few functional nerve cells in the brain. Those that can be found are mostly large and distinctive with positions and connectivity patterns that are consistent from one individual to another. Thus there are several pairs of 'Müller' cells linking the sensory region of the head with the motor organisation on either side of the trunk, and a pair of 'Mauthner' cells that are presumably related to the maintenance of equilibrium since they connect the spinal system with the roots of the eighth (auditory) nerve. In the spinal cord a relatively small number of sensory and motor nerves are linked by internuncial cells that are equally regular in position and connections. The whole system, comprising at most some hundreds of cells (compared with some millions in the adult), enables the animal to make co-ordinated swimming movements from the moment of hatching. It is a minimal system, with very little of the duplication of parts that ensures a high safety factor and the more elaborate gradation of responses in the adult, but nevertheless shows many of the features that must be fundamental in the construction of the fully developed adult structure. The cells tend to be arranged in pairs, segmentally, with internunciary neurones always intermediate between receptors and effectors. The larger cells of the brain have processes that penetrate to these segmental circuits and presumably superimpose a higher control that will influence what is going on in the segmental areas. The similarities between such an arrangement and the cardiac ganglion preparation discussed above are surely not coincidental and confirm that the essential gross functional similarity of nervous systems in vertebrates and invertebrates may well extend to details in the way these systems are arranged.

The above are cases where analysis is being made of integrative processes related to the motor output of the Central Nervous System (CNS). An alternative approach is to look for cases where the sensory input is integrated in a manner simple enough to be understood and correlated with the structure of the parts concerned. One case where it appears to be possible to do this was reported by Wells, who has studied the tactile system of *Octopus*. By training blind octopuses to make tactile discriminations between pairs of objects that differ in only one respect at a time we can investigate systematically what differences in objects touched are distinguishable to them. It transpires that octopuses can distinguish between objects differing in texture, or 'roughness', but not between objects that differ only in shape. We can rate the roughness of an object to *Octopus* in terms of the proportion of any part of the surface covered by the animal's suckers that is not actually in contact with them—the suckers are rather inflexible and tend to bridge hollows in the surface. We can create objects of varying roughness by cutting slots or holes into them. The percentage of the surface of such objects that is cut away is the percentage that the animal cannot touch, so that the difference between two objects can be expressed in terms of the difference between two percentages. We find that the proportion of errors made in discrimination experiments is related directly to the difference between the objects measured in this way, and that octopuses cannot be taught to distinguish between objects of equal roughness that differ only in other ways (e.g., by the orientation or pattern of grooves cut into them). It follows that the octopus must be classing objects simply in terms of the proportion of sense organs excited in the suckers applied to the surface of the objects.

The number of sense organs in the arms is greatly in excess of the number of sensory nerves entering the brain, so there must be a considerable summation of sensory impulses in the arms, and a considerable loss of potential information. From what we know of the anatomy and from a study of the local reflexes in the arms of *Octopus* it seems that summation must occur within the ganglia that are to be found in the arm above each sucker. Sensory axons ramify in these ganglia and intermingle with the processes of further cells that relay the information received up the arm to the brain. Since the animal does not make discriminations that would necessitate integration of information about the relative positions of its tactile sense organs (as it would have to in order to discriminate between shapes, for example) it seems likely that this relaying is limited to passing on some account of the proportion of sense organs excited. The task of the brain in tactile integration is therefore in all probability limited to the discrimination of different frequencies of discharge in the nerves coming in from the arms, objects being recognised by the characteristic frequencies resulting from contact with them.

We have, then, a very fair idea of what the animal must be learning to recognise about objects touched when we train it. We can also trace which part of the brain of the creature is concerned. The brains of cephalopods are composed of a number of lobes to a very considerable extent departmentalised in function, perhaps for reasons akin to those determining segmentalisation of function in arthropods. We find that a particular small pair of lobes (the inferior frontal and subfrontal lobes) appears to be exclusively concerned with the integration of tactile stimuli and with tactile learning[1]; their removal abolishes *Octopus's* ability to learn to recognise objects by touch but in no way interferes with visual learning. This means that in *Octopus* we are now able to state with some degree of accuracy not only *what* the animal learns but *where* it learns it. Needless to say the lobes concerned have themselves a complex structure and are composed of a very large number (in this case about six million) of small interconnected cells—a situation that one has come to regard as inevitable in any integrative area showing learning properties. This may mean that in order to analyse the function of *Octopus's* tactile system further we must fall back upon the wider, comparative approach to the problem of nervous structure and function. We do not know precisely what the learning part of the tactile system of *Octopus* is built to do (to show that the animal learns to discriminate between frequencies tells us nothing about how it does it) and we do not know which are the significant features of the complex structures that we see. While we can continue to work out the structure of these parts and determine by surgical means what is the minimal assembly of cells within the tactile system that will enable the animal to continue to learn, it is wise to survey learning systems elsewhere in the hope of finding common factors in their mode of function and in their construction that will tell us what to look for in the detail of these assemblies once determined.

The derivation of general principles of organisation from observation of a wide range of nervous systems runs into an immediate problem of how to describe the principles derived and, at the moment, this is perhaps the major stumbling-block in the way of the wider comparative approach to a study of learning systems. In the past a variety of descriptive methods have been fashionable and generally derived from the latest engineering techniques. Thus clockwork and plumbing analogies remained in vogue until the electrical nature of the nervous system was demonstrated; telephone systems replaced clockwork but have now become regarded as equally unsatisfactory—the CNS is more than a mere switchboard. It is now fashionable to describe the nervous system in terms of computers, and,

[1] Removal of the vertical lobe increases the number of trials necessary to attain a given standard of accuracy of response in tactile as in visual experiments; it does not prevent the animal from learning to make tactile discriminations.

as Taylor showed, this has certain advantages in as much as it is now possible to produce working models that not only fit such descriptions functionally but are also built up of units with properties analogous to those of nerve cells. He demonstrated how a model consisting essentially of a few dozen 'nerve' units arranged in a randomly connected network with input from a 'retina' of photoelectric cells can recognise shapes (in this case letters of the alphabet), producing the same output tone in a loudspeaker whenever the same pattern of visual stimulation recurs. The machine, moreover, can be trained to associate these visual patterns with 'auditory' stimuli fed into the network from a microphone 'ear'; after simultaneous occurrence of a particular visual and auditory input on one or more occasions it will produce the tone once fed into the ear when the visual pattern occurs alone. Models of this sort are useful for investigating the plausibility of hypotheses about the arrangement of neurones, and show how very few nerve units are necessary for systems to show the comparatively complex behaviour that we generally associate with much larger assemblies of neurones. As a means of describing the activities of nervous systems analogue computers suffer, however, from a trouble common to all languages derived from description of automata in that they necessarily imply a particular theory of how the system works. Taylor's nervous analogue showed learning properties because of changes in conductance at the 'synapses' between its randomly arranged units. It is quite possible that the nervous system works in this way, but it is also possible that memories are not stored in this form at all. They might, to mention just one alternative, be retained as continued activity in reverberating circuits. This sort of difficulty greatly reduces the value of electrical analogues as means of objectively recording observations on the organisation of nervous systems.

A means of getting round this difficulty of describing our observations has been proposed by Mackay (1956). He has suggested that a better way of describing the functions of the various parts of nervous systems, at least in general terms, is by means of information flow diagrams, which are noncommittal about the structural detail of the mechanisms involved. Pringle illustrated his talk on the analysis of nerve function with information flow diagrams, two of which are illustrated in Fig. 1. Fig. 1*a* is a diagram illustrating the minimal pattern of information flow required

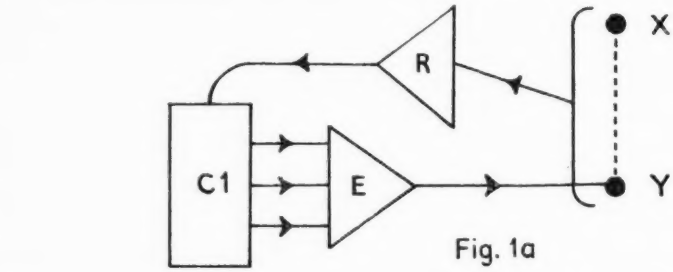

Fig. 1a

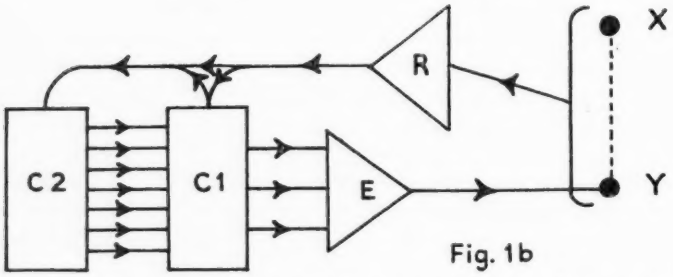

Fig. 1b

Fig. 1.—Information flow diagrams illustrating (*a*) the minimal pattern of information flow necessary for an adaptive system and (*b*) a flow pattern for insight learning (see text).

by an adaptive system. R is a receptor system that will signal when Y departs from the optimal state X, and C a controller capable of determining which of several possible actions shall be carried out by the effector system E. As Y departs from X, a 'mismatch' signal from R activates C. If all that is passed to C is this one 'bit' of information (i.e. that Y has departed from X), C can only direct that the possible reactions of E be carried out at random until, by chance, Y is returned to X. Such a system is likely to be useful only in the special case that the possible ways of Y leaving X are very few, and there is no necessity for gradation of the responses by E. In most cases the system can only be efficient if R signals to C not only the information that Y has left X but also some information about the direction and magnitude of the change XY. By integrating this information the controller, C, can switch on the appropriate reaction from E's repertoire. In a nervous system the advantages of a considerable concentration of the available nervous tissue into the controller, C, are obvious; a large amount of information from many receptors can all be used to control the operation of each effector and the adaptive performance of E finely adjusted to meet the requirements of situations in which the animal finds itself.

The performance of the system can be still further improved if C has some means of storing information about the history of previous departures of Y from X. This is true except in the event that the changes causing Y to deviate from X are random in direction and magnitude, a situation that is excessively unlikely because neither the animal nor its environment is randomly constructed; the probability of one type of event following another is rarely exactly 0·5 and the controller is able to accumulate experience that enables it to predict what is statistically likely to happen next so that an appropriate reaction from E is initiated as soon as the departure of Y from X is signalled. The advantages of a nervous system organised in this way to an animal that must adapt quickly to changes is that the animal can embark on a course of action statistically likely to be correct without waiting to collect all of the available information; this is one reason why in the normal way there is a very considerable redundancy of information coming into the CNS from the sense organs.

The controller can make predictions as a result of experience acquired during the lifetime of the individual or genetically acquired by its ancestors. Of the two ways of programming the controller individual experience obviously provides the animal with a more flexible instrument at the expense of increased risk while the creature develops its potentialities, and in practice we find that the nervous systems of animals invariably represent a compromise. The organism cannot be launched into the world with correct reactions to all the situations that it is likely to meet 'built in' or it will be helpless in the event that the future does not precisely resemble the past. It cannot, on the other hand, be born with its nervous system entirely 'blank' because it will never have time to work through all the possible trial-and-error reactions to situations as they occur, even if it survives the hazards of such a process. In practice even those animals like ourselves that depend in adult life almost entirely on learned rather than innate responses are born with a genetical memory determining that certain large groups of situations be classed alike and give rise to the same reactions. A baby tries to eat anything small enough to be got into its mouth and learns exceptions to the rule by trial and error. The baby has the enormous advantage that it starts off with one of the two alternative 'correct' solutions. Another (and safer) way of ensuring that an animal will survive while it develops its potential capacities is found in Cephalopods. *Sepia* hatches with its nervous controller in such a condition that it will only attack when stimulated by visual patterns closely resembling the small shrimps on which it feeds. As it grows up this selectivity relaxes gradually so that the animal increases the range of things that it will attack and learns to recognise as 'food' or 'not food' by trial and error (Wells, 1958).

The degree to which an animal comes into the world with its nervous system genetically programmed depends upon the sort of life that the creature has to lead. If it is to live in a very constant environment (sedentary animals, plankton) there is no point in it possessing the relatively large number of nerve cells that appear to be a necessary structural feature of highly adaptive nervous systems. As a matter of economics it simply is not worth the animal supporting this sort of system unless it confers some selective advantage over the smaller 'built-in reaction' type and we find that animals having nothing to gain from flexibility tend to have small controllers and few, fixed reactions. Animals that breed quickly and produce a great many offspring can afford to rely on genetically determined reactions provided that enough variation in these occurs to ensure that some individuals will survive if the future fails to resemble the past in all respects. Pringle (song of cicada, see above) has shown how slight this variation need be; alteration in the connectivity patterns of as few as one pair of neurones can produce very considerable differences in motor output. In animals with a small total number of nerve cells there is, of course, a relatively greater chance of small variations producing significant changes in behaviour so that animals with simple controllers can profit from a genetic source of behavioural variation not available to more slowly breeding species with fewer individuals necessarily equipped with more complex and adaptive systems.

In addition to learning from actual physical experience of their environment some animals can apparently arrive at the correct solution to new problems without observably testing the various possibilities open to them. We call this class of behaviour 'insight'. What sort of information flow pattern would be required for an organism (or machine) to behave in this way? One possibility is shown in Fig 1*b*. This is a modification of Fig. 1*a*, with an additional controller *C*2 that is related to *C*1 in the same way as *C*1 is to the environment. Since *C*2 is connected to *R* as well as to *C*1, it can store information about the results of the trial routines carried out by *C*1 and thus detect further correlations in the sequence of events. Suppose, for example, that there are four types of event that may deflect *Y* from *Z*, which we will call 1 2 3 4, tending to occur in a sequence 1234 for, say, eight times, followed by 1111, and so on. *C*1 will detect that event 1 is likely to be followed by 2 or 1 (and 2 by 3, etc.). *C*2, getting information from both *R* and *C*1, will further detect that a series of eight sequences of 1234 is likely to be followed by 1111, and its consequent effect on *C*1 resolve the difficulty that *C*1 cannot by itself predict whether 1 or 2 will follow 1 in any given instance. *C*2, in short, organises trial sequences from the repertoire of *C*1 in the same way that *C*1 organises routines by *E*. Now since there is a wholly internal loop between *C*1 and *C*2 the process of detecting correlations between past events can proceed even if no additional information is fed into the system. In insight learning where all the features of the new situation will have occurred before in some form or another (even though the particular combination of them represented by the problem is new), patterns of effector response suitable to the new situation can be evolved by an internal trial-and-error process.

The economies of such a mechanism considered as a nervous system enabling the animal to work out in advance the probable consequences of various actions by *E* are obvious, but is there any evidence that the nervous system is actually built in this manner? The answer would appear to be 'yes'. The flow diagram 1*b* is, of course, a simplification and *C*2 represents what would presumably be, in practice, a hierarchy of controllers, each abstracting from the experience of the one below. The characteristic features of this hierarchy are that it must be self-organising, since its function depends wholly on experience, and that it will have no direct control on the effectors. There are considerable areas in the brains of many invertebrates and of all vertebrates that have just these characteristics, the example *par excellence* being the frontal lobes of mammals. It is in these animals with large volumes of apparent self-organising nervous tissue that insight learning—'the solution of a

problem by the sudden adaptive reorganisation of experience' (Thorpe, 1956)—is found.

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PERCEPTION AND SKILL

At the Dublin meeting of the Association, Section J (Psychology) devoted the morning of Tuesday, September 10, 1957, to a symposium on 'Perception and Skill'. Mr. R. Davis (University of Oxford) described experiments on the interference between two stimuli delivered in rapid succession. Mr. D. E. Broadbent (Medical Research Council Applied Psychology Unit) gave a simple analogy to explain current theories of the mechanism underlying such interference, and Mr. J. Annett (University of Oxford) discussed the implications of such theories in the field of learning. Abridged versions of these papers are printed below in the order of presentation.

CHANNELLING OF AUDITORY AND VISUAL INFORMATION

By Roy Davis

Whenever a person performs a skilled task he is faced with a stream of signals, in the form of changes in the environment, and in accordance with these signals he has to organise the appropriate responses which constitute the successful performance of the task. The sort of task I want to talk about is one in which the operator cannot anticipate the occurrence of the next signal, and in particular I want to discuss the situation where he knows the type of signal which will occur and the sort of response which he will have to make to it, but doesn't know when it will happen.

Let us first consider the situation in which a single event occurs, to which the subject has to respond. For example, a light flashes on and the subject has to press a key as soon as he sees the light. This is a situation which will be familiar to most of you, and which is used for measuring the 'Simple Reaction time' of the subject.

What happens now, if, after the signal to make the first response, a second signal arrives, indicating that a second response has to be made? Can the nervous system deal with the organising of the second response as efficiently as it did the first? One of two alternatives might apply. The nervous system might operate (*a*) continuously, but with the inevitable reaction time-lag: i.e., for any signal that is put in, the appropriate response would be fed out at a constant interval afterwards; (*b*) intermittently. The lag is there just the same, but in addition, once the system has taken on the job of organising the response to the first signal, it will not accept any more signals to deal with until it has finished the first job.

Now I want to suggest that the central parts of the nervous system concerned with organising consecutive responses behave in an intermittent way.

Let me give a brief account of an experiment which supports this view.

The subject sits looking down a dark tube which takes up most of his field of vision. At the end of the tube are two neon bulbs. Each hand rests on a key and when the first light comes on he has to press one key, when the second comes on he has to press the other key. The interval between the two signals is randomly varied between 50 and 500 milliseconds.

The most important result is that when the interval between the two signals falls below 250 milliseconds the second reaction time increases sharply. It reaches a maximum value at the shortest interval of 50 milliseconds. Furthermore, for every

50 milliseconds by which the interval between the two signals is decreased, the delay in responding to the second increases by approximately the same amount. That is, it looks as though the central systems become blocked for a period of 200 milliseconds or so after accepting the first signal. If a second signal arrives during this period it has to wait to be dealt with, and the time for which it has to wait (which is the amount of delay we measure) is equal to the length of time which still has to elapse before the central systems have finished dealing with the first response. The system is behaving in a discontinuous manner and the period of intermittency is about one-fifth of a second.

So far we have been dealing with visual signals only. What happens if the two signals are not in the same modality, if, say, one is visual and one is auditory?

We have to face the possibility of the nervous system behaving in different sorts of ways: there may be no intermittency at all, there may be intermittency of the same sort, or the delays may be even greater when we are using signals in different modalities.

Using the same type of apparatus described for the first experiment, but substituting a click in a pair of earphones for one of the light signals, these possibilities were compared.

The overall picture is the same as for the visual–visual situation: a delay which increases regularly for intervals less than 250 milliseconds to a maximum at the shortest interval used (50 milliseconds). A similar picture also emerges when the order of signals is changed and the auditory follows the visual signal. That is, it looks as though the second alternative is the correct one. No matter by what modality the signals reach the central brain mechanisms a second signal cannot be accepted until the response to the first has been fed out, and the clearing-up process has taken place. This might be expressed by saying that in this sort of situation the human operator behaves as a single-channel system rather than having several channels acting in parallel.

A further question which might be asked is, 'Does the delay arise merely because the subject has to pay attention to a certain signal, or does it arise because the subject has in fact to make a response to this signal?' In order to answer this question two further experiments were performed. In the first of these experiments the apparatus and method was exactly the same as in the visual–visual experiment already described. The only difference was that the subject was instructed this time not to respond to the first of the two lights. The results of this experiment show very little improvement over the delays which occurred when he was responding to both signals. There is a slight shortening, of the order of 20–30 milliseconds, but most of the delay is still present. That is, the mere registering of a signal without performing any overt response to it is sufficient to account for nearly all the delay observed.

A final experiment which I want to describe consisted in getting the subject to make a 'response', as it were, without a signal having occurred. The warning period and the first signal were dispensed with, and the subject was told that he could set the apparatus going at any moment he chose by pressing on one of the keys. Following his pressing of the key, the light to which he had to respond came on at an interval which again was randomly varied between 50 and 500 milliseconds.

This time there was no delay shown in the results at any interval. The subject was just as efficient in responding to a signal which came 50 milliseconds after he pressed the first key as he was in dealing with a signal that came 500 milliseconds afterwards. That is, the actual performance of the response does not contribute to the delays observed, the source of the delay lies more to the perceptual side.

To summarise the conclusions.

1. In the sort of situation which has been considered, where because of the random arrangement of the time intervals the subject cannot learn when to expect

the next signal, he behaves as an intermittent system. After the first signal has been accepted, a second signal must wait until the response to the first has been organised and the supposed clearing-up process has taken place before it can be dealt with. The total duration of this period is about one-fifth of a second following the onset of the first signal.

2. The human operator functions as a single channel, at least so far as auditory and visual signals are concerned. The delay cannot be eliminated by using a different sense modality for the second signal.

3. The source of the delay lies on the perceptual side of the system. It is paying attention to a signal which matters rather than the performance of the response to it.

THE ROLE OF ATTENTION IN SKILL WITH A MECHANICAL ANALOGY

By D. E. Broadbent

As long as a man sees, touches, and handles his work, he is well adapted to it by nature, and we need no more than a traditional understanding of how he does it. But as soon as we replace his vision by dials, gauges and cathode-ray tubes, and confine his actions to button-pushing, we are making the situation unnatural; and unless we understand how our brains deal with incoming signals and translate them into decisions for action, we may present a man with a job that cannot be done.

Now the experiments which have been forced on us in this way have taught us a lot about perception. The best way of bringing these experiments together is probably by the language of communication theory. But this kind of language means rather little to some practical people, and also to many psychologists. Now one of the advantages of the language is that the same statement can apply to systems which are physically very different; an information store may be a magnetic drum, a punched tape, or a mercury line, and for many purposes it doesn't matter which. Equally, the statements we make about information flowing through a man could apply also to information flowing through a machine. Such a machine was described recently (in the *Psychological Review*) to make clearer to the uninitiated what some information theorists have been saying.

The machine consists simply of a Y-shaped tube, with a flap hanging at the junction of the two arms. This flap can be set to close off either arm, or left swinging freely. A set of ball-bearings is also necessary, each marked with a number to identify it, and each only just small enough to pass down the stem of the Y. The arms, on the other hand, are wider.

In this model, the arms are analogous to different sensory channels, and the bottom of the stem to a response. The balls represent the information contributed by stimuli: dropping a ball into one arm so that it runs down the arm, knocks the flap aside, and emerges at the bottom of the stem is analogous to delivering information at a sense-organ and observing the resulting effect in response.

The basic feature of the model is of course that when you drop balls alternately into the two arms they will happily emerge at the bottom: but if you drop two balls simultaneously one into each arm, they will strike both sides of the flap at once and jam. The consequences of this can be avoided by previously setting the flap to close off one arm: the ball on the other arm will then get through satisfactorily. In other words, you can do two jobs at once provided that crucial information from

one does not arrive at the same time as crucial information from the other. If that does happen, the resulting chaos can be cut down by a previous instruction to concentrate on one task. All these points have in fact been shown by experiment.

Now let us consider some other features of the model. Suppose two balls are dropped in, one just slightly earlier than the other. This slight difference in time will give that ball a disproportionate advantage, since it will knock over the flap and so secure admission to the stem of the Y. Similarly, in an air traffic control tower, if two loudspeakers suddenly deliver messages, it has been shown that a very slight difference in the time at which the messages begin produces a big difference in the efficiency with which the correct one is answered.

Another way in which one can increase the chances of a particular ball passing through the Y is by throwing it violently into one of the arms, while merely dropping the other ball into the opposite arm. The ball with the greater kinetic energy will, of course, force over the flap, and so appear at the bottom of the Y. Similarly, if a man is working at a control panel and two lamps light up, it is the brighter light which is more likely to secure response. A rather similar effect can be got by tipping the whole Y to one side so that one arm is more vertical than the other; balls in that arm will then stand a particularly good chance in competition with those in the other. Similarly, some of our sense-organs have higher priority than others. If one wishes to secure response from a man by using a pin, it is not so effective to do it by dropping the pin and stimulating the auditory nerve as it is to stick the pin in him and arouse pain fibres.

Now let us consider an example of more subtle points. Suppose you have a set number of balls. How should you put them through this model: all in one arm, or half in each ? Obviously the latter system is more likely to produce a jam. The same is true of air traffic control systems; if a given number of messages enter a control tower, the worst arrangement is to have them divided equally between the various radio channels. It is a better situation to have most of them on one channel. It is possible to go on in this way, drawing more complicated analogies with behaviour. But these details are available elsewhere, so I only want to make one last factual point, and then consider more general questions about this approach.

This concerns the effect of speed of stimulation. If two balls are inserted with a very brief time interval, so that the second ball starts to enter the arm before the first is fully in, they can enter the Y but cannot both pass down the stem. The second one will therefore be delayed and will only pass down the stem after the first one has done so. The second of two closely adjacent and information-bearing stimuli will therefore give rise to a reaction only after a delay: and this is the effect which Mr. Davis has already discussed.

Now let us turn to more general points. First, one ought to emphasise that in this model the balls represent information in the technical sense, and not stimulation. That is, if a stimulus is very highly probable at a given time in a given situation, there will be no ball corresponding to it. If a skilled man takes hold of the controls of a lathe, the resulting touches and pressures on his hands convey little information, and so do not distract him from watching the tool cutting the work. This leads on to Mr. Annett's paper.

A second general point concerns the difference between this approach to attention and earlier ones. If this account seems to you obvious, and hardly worth saying, I shall be pleased for two reasons. On the one hand, the theory expressed by this model cannot be in violent conflict with everyday experience if you find it obvious. But on the other hand, you have only to consult any text-book, such as Woodworth's *Experimental Psychology*, to find that everyday experience does not force a view of this sort upon us. Some theories disregard attention altogether, some regard it as a state of conscious experience, some as an adjustment of the senses to allow particular stimuli entrance. All are very much worried by such facts as that

a man may actually do mental arithmetic better when tapping rhythmically with his free hand than he does when performing only one task. To an information theorist, of course, this is no mystery because rhythmic tapping demands little or no transmission of information through the nervous system, and therefore does not interfere with other tasks that do require such transmission. If this view seems to you obvious, then it means that the model has done its work well, since the theory it conveys has not historically been obvious.

Theories of this general type lie behind the sometimes forbidding language of information theorists, and they are raising anew problems which have lain neglected since the great days of introspection. Perhaps it may be worth your while to learn the language.

PERCEPTUAL ORGANISATION IN SIMPLE SKILLS

By J. Annett

A skilled performance of any kind, whether it be in the workshop or on the games field, gives every evidence of organisation. The craftsman or the trained athlete works with speed and precision and yet with great ease. He knows precisely what to look for and when. The new trainee, on the other hand, may know *what* it is he has to do without having learned *how* to do it. When he grasps the controls of a machine for the first time nothing feels quite as he expected it to feel. Yet after weeks or months of practice a smooth and skilled performance is achieved.

All the sensory messages which impinge on the operator we will call the input signals. These include not only such things as dial readings or the sound of a motor, but also things like the 'feel' of a control, the tension of a piece of cloth, and all the stimuli which are fed back to the operator from his own musculature whilst he is doing the job. A random set of input signals would be a totally unorganised set of signals. The point I want to make here is that the basic datum which the brain has somehow to organise is not such a random set.

A physically sensed object has some internal consistency, it is bounded by fairly predictable contours and its surfaces exhibit law-abiding gradients of texture. As the observer moves through the world the pattern of input signals goes through a highly systematic set of transformations. Furthermore, input signals from different sense channels tend to be very highly correlated. The relationships between sets of input signals do not change at random.

Information theory can be of great help in considering organisation, so I am going to introduce one or two very straightforward concepts. In a general way we can say that something which happens unexpectedly gives a lot of information and something which is predictable gives very little information. If you are pretty certain that a particular event will occur, you are not much wiser when it actually happens—you have gained little information. The complementary statement is that a highly expected signal is redundant.

It would follow from this that a random set of signals would contain an infinite amount of information, but we know from many recent studies that the human brain is severely limited in the amount of information it can deal with. For the sake of comparison it has been estimated that the information capacity of a television channel is 50,000,000 units a second, a telephone can handle 50,000, but the most that a human operator can be shown to handle is a mere 50 units per second. It

should be fairly obvious that if the input signals were anything like random the brain would be intolerably overburdened.

Now, all this has important implications for the perceptual or input side of skills. In a routine repetitive skill we have probably the best example of a very highly organised or non-random set of input signals. As a task is practised the same sets of input signals occur over and over but with some element of variation.

If such a series of signals, *A B C* . . ., are repeated regularly, then the occurrence of *B* and *C* will soon become highly probable whenever *A* occurs. In information-theory jargon *B* and *C* become redundant and the information which was originally conveyed by the whole series will tend to become concentrated at the beginning of the series. There is therefore much more information for the new trainee to deal with than there is for the old hand.

There is a further reason why this is true. You will remember that I included signals coming from the operator's own musculature in the input signals. The trainee who makes varied or partly random attempts at a movement is, in effect, feeding into the input a lot of unpredictable signals, so his job of recognising what follows what is even more difficult. He may, by virtue of his own responses, present himself with non-recurring or partially randomised series of input signals and he consequently has to deal with very much more information than the skilled operator, who is, superficially at least, working faster and doing more. The trainee's task is literally harder for it is never the same task twice.

The approach to the understanding of the perceptual aspect of skills which I have tried to outline has some useful connotations in applying actual training schemes. A problem which has bothered psychologists and trainers for many years is whether a trainee faced with a complex task should be taught small parts of it separately, or whether it is better to practise the task as a whole from the beginning. Part of the problem is how to make appropriate divisions of a task. Following from what I have been saying we may draw a conclusion which is superficially a paradox. If parts of the task are highly interdependent they should be split up and trained separately. If, however, there is little interdependency, nothing is lost by practice on the whole task. The reason for this lies in an appreciation of what the trainee's task actually is. He is trying to learn a stable sequence of events. If his own errors on one part of the task alter what he has to do in the next part, he will not be presented with a stable series of events—he will be trying to learn a non-recurring sequence.

Another field where the new approach to skills is relevant is the problem of the use of training devices to give the trainee guidance and immediate knowledge of results. Some experiments recently carried out at Oxford demonstrate how careful we must be in using devices to give trainees extra cues. Such cues must be useful and informative in the early stages of training, but they must also become redundant before the trainee can move on to the actual task without experiencing a sharp drop in performance.

I will give a brief description of one of these experiments. The subject's task is a moderately difficult one. He has to learn to exert a precise pressure of 500 grammes on a rigid metal bar, whilst looking at a moving light which shows him at any moment just how hard he is pressing. After practice there is a test session in which the light is removed and we see how well the subject can remember the pressure. The result is that it is misjudged, often as much as by 100 per cent. However, if with the same set-up and the same task the signal from the screen is delayed by a short interval so that the subject first receives pressure signals from his fingers and then the extra signal from the screen, then learning is very good.

This experiment illustrates that the temporal structure of the input signals can be crucial in the training situation. It is quite possible that an otherwise useful training device can fail in its objective on this account.

Let me try to summarise. In studying skill the most obvious thing to investigate is the motor response—the output. Yet prompted by information theory recent investigators have looked more closely at the receptor aspect or input. Using the notions of information and redundancy we can reach a better appreciation of the amount and kind of organisation which occurs on the input side of skilled performance. The input signals are already highly organised, and the task of the operator is to appreciate the organisation which is already there. During practice many input signals become highly predictable, so that the operator, who is limited in the amount of information he can deal with in a given time, has progressively less information to deal with; his task becomes easier as he becomes more skilled.

INCENTIVES AND COMMUNICATIONS IN INDUSTRY

by

S. B. N. SHIMMIN, L. J. BUCK and R. SERGEAN

Introduction

This article describes three papers read by members of the Medical Research Council's Industrial Psychology Research Group to Section J (Psychology) on the afternoon of Friday, September 6, 1957, at the Dublin meeting of the British Association. Each paper was based on work sponsored by the Joint Committee on Human Relations in Industry of the Department of Scientific and Industrial Research and the Medical Research Council, and was financed from Counterpart Funds derived from United States Economic Aid. Although they were presented consecutively the papers were not written as contributions to a symposium; they are therefore summarised under separate headings, but first an account is given of the general background to the investigations.

Over twenty years ago Elton Mayo (1933) declared that 'psychology is beset, to an extent probably greater than any other study, by a tendency to substitute words for careful observation' and the same is true of human relations today. Many generalisations are made, some of them self-evident, which are of little help in dealing with specific problems. For example, the statement that 'effective communication depends upon an atmosphere of mutual trust and confidence' needs careful definition if it is to become more than a high-sounding phrase. One requires to know what is meant by 'effective' in this context and what kind of information is transmitted. It is true that freedom from suspicion and an atmosphere of trust are extremely important in negotiations and decisions concerning people, but there are many situations where goodwill is not enough and factual information is vital. Successful communication, in the sense that meaning is conveyed and intended action taken, can also occur when liking and respect are conspicuously absent. Similarly, discussions of incentives are apt to assume that 'team spirit' and 'a sense of justice' are of the same order as bonus payments and may legitimately be compared with them. No one would deny that level of earnings affects a worker's job satisfaction but, as Baldamus (1951) points out, it is unrealistic to try to decide which is the more important when the former can be manipulated and controlled and the latter is intangible.

These are some of the reasons why studies of human relations are often criticised as inconclusive. Another is the failure to recognise an essential difference between the interests of research workers and people in industry. The latter usually look for a quick solution to a problem as they see it, whereas the former wish to investigate the relevant variables. Each group asks different questions in a given situation and the data obtained by one are not the answers sought by the other. Hence the results of research are not always suitable for direct application—a fact which bewilders executives and others who look for specific recommendations. It was to try to minimise the danger of such misunderstanding that the Joint Committee sought projects likely to contribute to practical knowledge of industrial problems.

The immediate post-war years saw changes in management structure as a result of expansion and development in many industries. At the same time there was renewed interest in financial incentives as a means of encouraging the higher productivity needed by the country. These trends were the subjects of the studies described here, the first of which deals with organisational factors affecting the flow of essential production information and the second and third with certain aspects of incentive payment systems. In each case a relatively precise problem

was chosen for investigation on the basis of previous research findings and laboratory studies. For example, in the sphere of communication, a number of attitude surveys had shown that managers and supervisors often felt hampered in their work by lack of information, and laboratory experiments suggested that it would be worth examining the problem of knowledge of results in an industrial setting. A study was therefore made of the formal communication pattern in four similar factories in relation to estimated delivery dates. This was carried out by Mr. R. Sergean and described in his paper 'Decision-making and the Presentation of Information'. It is summarised below under the following heading:

Effects of Communication Structure on Delivery Estimating

Communication, in the sense that information is passed from one place to another (Miller, 1951), is normally affected by three types of variable—personal relationships, social relationships and organisational structure. In the laboratory the effects of linking members of a group in different communication networks may be studied under controlled conditions. The same situation may also be examined in a factory, where behaviour is influenced by the formal structure of management, but here the position is complicated by social interactions usually absent in a simple, laboratory experiment. One class of information, however, must be transmitted whatever personal or social barriers may exist within a firm. This is the essential production information required for daily operational decisions and for fulfilling customers' orders. Communication of this kind is only minimally affected by interpersonal and social variables and it thus offers the best opportunity for the study of organisational factors.

As part of a wider investigation of communication problems in industry, a study was made of variations in the formal communication patterns of four light engineering factories all carrying out the same type of work. These patterns were considered from the viewpoint of people in the factory who had to make decisions from the production information available to them. 'Decision' here does not mean an occasional activity or a single judgment, made perhaps once in a lifetime, the success of which may not be apparent until much later. It refers to the day-to-day judgments in planning and production control departments, that is to frequently made decisions of a similar kind, the effectiveness of which depends on knowledge of earlier decisions in the series. The particular decision examined was the estimate of delivery—the length of time judged necessary to complete a customer's order. Accurate delivery was especially important for the firms studied because their customers were manufacturers who also had delivery dates to fulfil. Hence an error in estimating was liable to cause double confusion, first in the production departments of the firms themselves and, secondly, in those of their customers whose production programmes rested on the estimates received.

In comparing the communication structures of the four firms, three questions were asked: What was the position in the organisation of the person whose job it was to estimate delivery time? In what way did this position affect the information available to him? Was it calculated to increase or to reduce the likelihood of error in his estimates? •

The firms fell into two distinct pairs. In W and X delivery time was assessed by works estimators on the shop floor, who were responsible not only for the estimates but also for ensuring that the delivery time was fulfilled. In Y and Z estimating was carried out by office staff, who were physically isolated from the shop floor and had no responsibility for keeping the promised delivery time. This was the function of a separate works control department which, in turn, took no part in the estimating process.

Comparisons were made of the estimated and actual delivery times in each of the firms for all orders received from customers over the same four-weekly period.

The number of days by which a completed order exceeded (−) or fell short of (+) the estimated time gave a measure of the accuracy of the estimates. Table I shows the range of error for each firm and a condensed distribution of errors within this range.

TABLE I[1]

Errors in delivery estimates: (days)

Firm	Estimates		Range of error	Percentage frequency of error (+ and −)				
	No.	Range		0–9 days	10–19 days	20–39 days	39 + days	
W	663	2 to 170	− 214 to + 78	42	18	22	18	100
X	338	2 to 185	− 197 to + 74	26	24	29	21	100
Y	540	3 to 205	− 187 to + 149	23	22	26	29	100
Z	461	3 to 256	− 198 to + 115	19	15	30	36	100

[1] Reproduced by kind permission of *Nature*.

A more refined firm-by-firm comparison was also made from the complete frequency distributions of error for each firm. Using Whitfield's (1947) modification of Kendall's *tau* method of rank correlation, the order of accuracy in delivery estimating was W, X, Y, Z. One explanation of the more realistic estimates of firms W and X is that their works estimators were in close contact with the shop floor and were aware of day-to-day manufacturing difficulties. Their position in the factory enabled them to know the consequences of their estimates immediately, directly and continuously. In firms Y and Z, on the other hand, any knowledge of results which reached the office estimators appeared to be retrospective, indirect and intermittent. Delivery estimating involves a fairly close succession of similar judgments, the success of which is dependent on knowledge gained from previous decisions. If the communication structure of a firm keeps the estimator well informed of the results of his actions the chances of accurate delivery estimates are likely to be increased.

This is an important finding, because organisational variables in the communication process are apt to be discounted. The tendency in all four firms was to regard errors in delivery estimates as due to unforeseeable circumstances or to factors outside their control. Only rarely was it suggested that the firm's planning arrangements might be at fault. While material shortages, labour difficulties and pressure from the customer undoubtedly complicate the decision-making process and make estimating more difficult, these conditions are fairly uniform at any one time for firms producing the same goods in the same market. It is clear from this investigation that estimating error may be reduced by revising the formal communication system within a factory. Not only will this make for more effective decisions, but it is also likely to lead to improved morale. Better information on which to base his decisions reduces stress upon an estimator, and the more accurate he makes his estimates the easier will be the task of foremen and workers.

Knowledge of results of performance is also important in connection with incentive payment systems. This was shown in the second paper, given by Miss Sylvia Shimmin, which is outlined here.

WORKERS' UNDERSTANDING OF INCENTIVE PAYMENT SYSTEMS

Systems of payment by results are designed to reward workers according to the amount of work done. Any increase in output brings a corresponding increase in

earnings, so that workers have a direct financial interest in their productivity. Assuming that people can and will work harder to earn more money, the success of an incentive payment system depends in part on how easily workers can perceive the relationship between work and payment. Much of the incentive value is lost if they do not understand how variations in bonus earnings reflect variations in working effort. For this reason industrial writers have invariably stressed the need for simple bonus schemes which are readily intelligible to workers, but many of the systems in use today still have an extremely complex structure. The enquiry described here was undertaken to see how well a complicated wage incentive was understood by industrial operatives.

The investigation was carried out in six mass-production factories, each of which used a modified form of the Bedaux system of incentive payment. Definition of the word 'understanding' presented an initial problem because, in all the firms studied, the bonus system was based on standards derived from time-study procedures. A knowledge of this was not essential for the operator to calculate his bonus, but it could not be omitted from a complete account of the scheme. As a result of pilot investigations it was found convenient to distinguish between 'formal' and 'functional' understanding. *Formal understanding* was used to denote knowledge of the principles of an incentive payment system, including the methods of work measurement and the calculation of bonus earnings. *Functional understanding* was the term used for a working knowledge of the relationship between effort and reward, that is of the cash value of given quantities of work based upon practical experience of the operations concerned. In the factories studied, formal understanding was tested by comparing workers' explanations of their payment system with the 'official' explanations provided by the firms. Functional understanding was assessed by comparing workers' estimates of their daily bonus earnings with their actual earnings. A full account of the methods and results is given in Shimmin (1958).

On the whole, workers had only limited formal knowledge of their incentive payment systems. Most of them were familiar with administrative details, such as who was responsible for booking and checking their work and what should be done to query a bonus payment or a work value. They also knew that work values were set by time study, but they did not understand the principles of work measurement. Very few operatives could explain exactly how their bonus was calculated, and those who were able to do so were usually shop stewards or workers' representatives with some experience of collective bargaining. On the other hand, there were very few workers without some method of reckoning their earnings, usually because they had a functional understanding of the system.

Functional understanding appeared to be the result of practical experience of a particular operation rather than of formal instruction. Workers who had 'got the feel of the job' found that they were able to judge their bonus earnings fairly accurately without conscious effort or calculation. Thus many of them gave good bonus estimates even though their formal knowledge of the payment system was poor. Conversely, some who could describe the system well could not estimate their bonus with accuracy. It was apparent that formal and functional understanding were not related. Functional understanding was facilitated by consistency in work and earnings, but it was of little use where the work was varied or where the operators were moved from job to job.

From the workers' point of view, satisfaction with an incentive system seemed to be a function of how well they could explain to themselves all contingencies experienced under the system. Apparent anomalies, such as more favourable bonus rates on some jobs than on others, or instances where extra payment did not seem proportionate to extra effort, were found in all the firms studied. Whenever these occurred they presented a problem of 'understanding', to which workers responded by trying to provide a meaningful frame of reference. If they were able to do this

to their satisfaction they usually rated their understanding as good. This meant they ceased to ask for more explanation and so a number of erroneous beliefs were established on the shop floor. For example, two workers in different firms reported that 'bonus is best on goods which yield the highest profits'—a view which amazed the time-study departments, but which seemed a rational explanation to the workers concerned, who could account in no other way for their varied earnings on different jobs.

These results show that if a complex incentive payment system is used, it is unlikely to be understood by workers and may become mistrusted in consequence. Most of the firms made careful attempts to explain their bonus schemes to the operatives, but mere formal explanations do not seem sufficient to ensure adequate understanding. So much depends on the needs of working situation, the type of information available and when, and by whom, it is given. For example, the worker who is already familiar with his job, and who then receives an account of the bonus scheme from the executives responsible for it, has an obvious advantage over the newcomer to the work who gets only piecemeal explanations from his supervisors and fellow workers. Some degree of functional understanding may be expected to develop with experience, but a worker may regard this as a poor substitute for more formal knowledge of the method of bonus payment. A firm is unwise to assume that operatives who can check and query their bonus earnings neither need nor desire further explanations of the system; indeed, the interviews showed that misunderstanding and mistrust provoked some queries 'just to keep the wages office on its toes'.

The problem is therefore one of communication. It is not suggested that the new employee in a factory should be given a condensed time-study course to prepare him for work on bonus, but it is desirable that he should know how much he will earn under different conditions and why his bonus may be more on one day with a long machine breakdown, than on another with few or no interruptions. What is needed is some method of integrating formal and functional understanding so that, on the one hand, established workers can discuss the incentive payment system more readily with managers and supervisors and, on the other, a more effective method is available for instructing new employees in the practical aspects of the scheme.

The third paper was by Mr. Leslie Buck, entitled 'The Effectiveness of Group Wage Incentives'. It was concerned with a modification made in the group bonus system at a railway carriage repair works, and is summarised under the following heading:

The Effects of Modifying a Group Bonus System

Piecework is an old and favoured method of payment by results, but its age does not make it faultless. Like other forms of bonus payment, it may need revision from time to time in order to retain its incentive value. This study examines the effects of a change in a group piecework system in relation to the structure and productivity of the groups concerned.

Four gangs of coach bodymakers, employed on servicing railway carriages, were paid according to the amount of work completed by each gang. Each man received a proportion of his gang's total piecework earnings for the week and a cost-of-living allowance based on the number of hours he had worked. Some time previously, part of the cost-of-living allowance had been consolidated with the piecework earnings so that the latter formed a greater proportion of the total wage. It was hoped that, by making wages more dependent on the work done and less on the number of hours worked, there would be a greater incentive to increase output. Both management and workers expected a rise in output and earnings as a result of this change.

Weekly productivity indices for each gang were examined for the periods before and after the change. These indices were derived from the piecework earnings and gave a measure of the work done per man-hour. Table II shows the rates of productivity increase for each gang before and after the payment system was revised.

TABLE II

Rates of productivity increase: units of productivity per week

Gang	Before change (56 weeks)	After change (247 weeks)	Difference
A	0·081†	0·045†	−0·036
B	0·065†	0·049†	−0·016
C	0·030*	0·063†	+0·033*
D	−0·007	0·069†	+0·076†

* Differs significantly from zero at probability level of 1 per cent.
† Differs significantly from zero at probability level of 0·1 per cent.

In gangs A, B and C productivity was increasing before the change, so a subsequent increase in output was not necessarily the result of an enhanced incentive. After the change, however, the rates of increase in A and B were almost unaltered—they even fell slightly but not to a significant extent. In gangs C and D, on the other hand, there was a clearly marked improvement in the rates of productivity increase. The new payment conditions thus had a differential effect on the four gangs, two of whom responded to the changed financial incentive and two of whom did not. It is difficult to isolate which feature of the change was the most potent, primarily because there is no control of the variables in a field situation.

A rather more definite result was obtained in relation to the structure and membership of the four gangs. A and B were relatively large gangs and C and D were much smaller. The average numbers of bodymakers employed in A, B, C and D were 41, 39, 16 and 9 respectively. This order corresponds exactly with that obtained for the pre- and post-change differences in rates of productivity increase. In other words, the increased financial incentive was more effective for the two smaller gangs. The gangs also differed in the stability of their membership, measured on the basis of periods of uninterrupted service. This is shown in Table III.

TABLE III

Discrete periods of membership: percentages in each category

Gang	No. of weeks unbroken membership				
	1–5	6–15	16–50	51–303	1–303
A	25	24	25	26	100
B	26	26	26	22	100
C	60	10	8	22	100
D	58	14	10	18	100
All gangs	35	21	21	23	100

It will be noted that both C and D had a very high proportion of short-service members, that is with only a few weeks' unbroken service, whereas in A and B short and long periods of continuous membership were evenly distributed. This is discussed at length elsewhere (Buck, 1957). The point of interest is that here again the pairing of the gangs corresponds to that for the rates of productivity increase.

It would seem from these results that the success of modifying a group wage incentive system depends in part on the characteristics of the groups to which it is applied. Hence it is not sufficient to consider the characteristics of the system itself: the probable outcome must be judged in terms of the structure and composition of the groups it is hoped to influence.

Conclusion

In concluding this account of three separate studies certain common features may be noted. Each investigation dealt with a particular human performance—estimated delivery time, estimated bonus earnings and the output per man-hour of a working group—which could be measured directly on the basis of field data. The methods used are suitable for the study of similar problems in other factories and some of these have already been undertaken. The results generally confirmed the findings of previous investigators, but they were not anticipated by the firms concerned. Large companies, like individuals, tend to blame external difficulties for failures which are largely their own fault. They were therefore surprised to learn how the behaviour of different groups could be influenced by organisational factors and by the quantity and quality of available information. Not every industrial problem can be reduced to a question of structure and communication, but it is suggested that in seeking ways of improving industrial efficiency detailed examination of day-to-day activities is an essential preliminary step.

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SCIENCE IN SCHOOLS

THE problems of the national need for more scientists and technologists and the need for the inclusion of science in the school curriculum as an essential component of general education can only be solved if more science teachers can be recruited and if adequate accommodation and facilities for the teaching of science can be provided in the schools. These problems were discussed at a Conference organised by the British Association which was opened by Lord Heyworth and held in the hall of the Royal Geographical Society on April 17 and 18, 1958. The Conference was attended by over seven hundred persons drawn from local education authorities, schools, training colleges, universities and from industry.

Sir Solly Zuckerman discussed the national need and estimated that the output of science and technological graduates must be doubled, i.e. increased by ten thousand during the next ten years if the output of industry continued to rise. Sir Eric James discussed the place of science in the school curriculum and emphasised that 'we have got to recognise that no education can be considered complete today which does not contain an element of science in the same way that we include English or history or mathematics' and stated that all curricula should be so arranged that all suitable pupils have a four or five year course in elementary physics, chemistry and biology to the ordinary level of the G.C.E.

Miss E. M. Huxstep referred to the fact that girls spend less time on science than boys and a much smaller proportion of girls choose to specialise in science and as a result there is less science accommodation in girls' than in boys' schools. She spoke about the great difficulty of getting science mistresses of good quality and referred, as did Sir Eric James, to the problem of what to take out of the curriculum to make room for more science. The problem of the supply of science teachers was dealt with by Dr. A. W. Barton. He referred to the fact that before the Second World War the grammar schools were well staffed with graduate science teachers. Today, 1,100 out of 7,160 posts are either unfilled or unsatisfactorily filled and the position of the secondary modern schools is just as bad: there are 1,793 posts unfilled or unsatisfactorily filled. Dr. H. F. Boulind, discussing the problem of accommodation and equipment, stated that less than half of the maintained grammar schools are provided with adequate lecture rooms and apparatus as judged by the standards of the Ministry of Education and more than three-quarters of these schools are inadequately provided with laboratory technicians including one-quarter which have none. He stated also that ten shillings per annum per pupil doing science is regarded as the absolute minimum for the provision of apparatus and consumable materials and pointed out that half of the maintained grammar schools received only eight shillings and some even less. He stated that the secondary modern schools are even worse off than the grammar schools in all these respects. Dr. J. W. F. Hill and Dr. B. E. Lawrence spoke about the efforts being made by the local education authorities to meet the situation. They referred to the major developments that had taken place during the past ten years and to the immense problems still to be solved.

Dame Kathleen Lonsdale expressed the view that many science teachers would be recruited if more women could be encouraged to read science and suggested that, in her view, it would be desirable for undergraduates to enter the universities at seventeen years of age and take a general degree course in three science subjects before proceeding to higher specialised degrees. Dr. Chesterman referred to the developments which were likely to result from the institution of a three-year course in the training colleges. Sir Raymond Priestley in the final session stated that one requirement for the solution of the problems which had been discussed is a very considerable increase in national expenditure on education and that the necessary money could be obtained if expenditure on non-essentials was reduced.

These are only a few points made by a few speakers. The discussion was lively and informed; the remarkable developments since the war were acclaimed and the major problems still to be solved were clearly defined. The full report of the Conference will be published by Messrs. Butterworth & Co. Ltd. and is a document of major educational importance. It should be read by everyone interested in the future of this country.

BIOLOGY OF CANCER

SECTION D (Zoology) devoted the whole of Friday, September 6, 1957, at the Dublin Meeting of the British Association to a discussion on the biological aspects of cancer. The session was introduced by Professor A. Haddow, Director of the Chester Beatty Research Institute. Professor E. S. Horning, also of the Chester Beatty Research Institute, then presented a paper on 'Hormones and Cancer'. He was followed by Dr. A. Glücksmann of the Strangeways Research Laboratory at Cambridge, whose contribution was entitled 'Cancer as a problem of cell differentiation'. Dr. E. H. Mercer, Chester Beatty Research Institute, contributed a paper on 'The electron microscope and cancer', and Dr. R. J. Goldacre, Chester Beatty Research Institute, a paper entitled 'The reaction of the cell membrane of *Amoeba proteus* with carcinogens'. Dr. M. Abercrombie of University College, London, spoke on 'Cancer as a problem of the control of cell movement'. Drs. G. C. Easty and D. M. Easty, Chester Beatty Research Institute, presented a paper, which was illustrated by a film, on the 'Specificity of normal and malignant cells'. Professor P. C. Koller, Chester Beatty Research Institute, then contributed a paper entitled 'Chromosome variation and cell polymorphism in malignant growth'. The symposium ended with a contribution from Professor A. Haddow on 'The general biology of cancer'.

The following account of the symposium has been prepared for publication by Dr. E. J. Ambrose.

Cancer arises from the uncontrolled proliferation of cells derived from the tissues of the host. For this reason, biological studies of cancer are mainly concerned with problems of growth and its control. This approach to the problem was clearly stated, at the Dublin meeting of the British Association, by the Chairman of the morning session, Professor Rogers Brambell. He pointed out the connection between studies of protein synthesis and abnormal growth in cancer cells, while Professor Haddow, in his introductory remarks, stressed the similarity between the behaviour of embryonic and cancer cells; he emphasised the need for more information concerning the development of specific regulating enzymes during embryonic development and differentiation.

Let us examine for a moment, some of the general aspects of this problem. The growth of unicellular free-moving organisms such as bacteria and protozoa will continue in an unrestricted manner provided that an unrestricted space, supplies of fresh media and oxygen are maintained. The cells grow and divide into two daughter cells continuously. In the higher organisms, this ability to proliferate is still maintained by most organisms even in the adult stage as can be seen during wound healing. But the process of growth eventually ceases. There are three possible ways of considering how growth can be controlled, i.e. a change in the medium surrounding the cell, a reaction between the cells and its neighbours, or a change within the cell itself. These three aspects were considered in the Dublin session.

The humoral factors which are of importance have been called chemical messengers. These hormones are secreted by glands, in various parts of the body, as for example the thyroid and the pituitary. They are then transmitted via the body fluids to various tissues, leading either to stimulation or inhibition of activity. But this response is highly specific, in many cases only a particular type of cell will respond to a particular hormone.

Some cancers, as Professor Horning mentioned, are produced as the result of a

hormonal imbalance, the presence of an excess of a hormone in the body fluids, leading to the active proliferation of a particular tissue. Such tumours are said to be hormone dependent. If the hormonal stimulus is removed, for example by removal of the gland which produces the hormone, the tumour may regress. It has now become possible to study such tumours in the laboratory. If male hamsters are treated with the female sex hormone, stilboestrol, it is found that tumours appear in the kidney. But these tumours are dependent upon the presence of stilboestrol for their maintenance. They can actually be transplanted if the animal has previously been treated with stilboestrol. But hormone dependent tumours may eventually change their character and be no longer dependent upon the presence of oestrogen for their maintenance. They are then said to be autonomous tumours.

An interesting example of such a tumour is an experimental tumour of the prostate induced by application of 20-methyl cholanthrene. When first produced, many of these were carcinomas, dependent upon the presence of the hormone, an androgen, for their maintenance as transplants. But they later became autonomous and were no longer dependent upon the androgen for their maintenance. The hormonal aspect of cancer is of considerable importance in therapy. Professor Haddow, and, later, Professor Huggins in the United States, have applied the principle of hormonal control to cases of human carcinoma of the breast. A number of these tumours are hormone dependent and can be controlled by reducing the oestrogenic stimulus.

Let us now consider the second aspect of the problem, the interactions between neighbouring cells. Such interactions are clearly observed during normal embryonic development and in wound healing, as the tissues begin to build up distinct and characteristic structures. Before examining these cell–cell interactions in detail let us consider the morphology of these structures. When a normal egg is fertilised it begins to divide. The daughter cells divide further and produce tissues of differing character in various regions of the embryo, heart, lung, nervous tissue, etc. This process is known as differentiation. To begin with, the embryonic cells have the potentiality to develop into any one of these particular tissues, but as the embryo develops the cells lose this potentiality and acquire the character of the particular tissue of which they are composed. Dr. Glücksmann described the changes in the structure of tissues which are seen during the growth of tumours. In this case there is an interesting progression in the opposite direction. As the tumour acquires increased growth potentiality the cells and tissue structure lose their character and there is a return to a more primitive form. Dr. Glücksmann described how this loss of differentiation can be particularly clearly observed in the epithelium. In the adult, the surface layers of the skin are continually being lost. They are replaced by continuous division of the cells in the basal layer of the epithelium. In normal conditions there is a nice balance between the rate at which cells are being produced in the lower layers and the rate at which they develop or differentiate into cells of other types in the surface layers. When a carcinoma appears there may be a disturbance both in the quantity and in the quality of this differentiation process. With slowly growing tumours there may be only slight loss of structure but in highly anaplastic cases there may be an almost complete loss of all organised structure. This aspect of cancer is also of therapeutic importance, because some radiation and other treatments may cause decreased rate of growth and also some tendency for the cells to rebuild the normal differentiated structure.

But apart from these general histological observations, is there any more direct method of studying cell–cell interactions? The growing of cells in tissue culture provides such a possibility and Dr. Abercrombie described some interesting results which have been obtained by microscopic study of cells kept alive in tissue culture. It becomes clear that the cells exhibit a considerable degree of movement. It is found that the direction of moving fibroblasts in culture is, however, not unrestricted.

When a cell is moving in a particular direction and makes contact with another its movement in this direction is inhibited; its direction of movement in the regions where it is not restricted by its neighbours may therefore become predominant. This control of movements by contacts has been called contact inhibition by Abercrombie and Heaysman.

Wound healing is an interesting example of the way in which contact inhibition operates. When the wound is first formed, the cells move out freely to fill the space, but as they make contacts with their neighbours these movements become restricted and controlled. The movements of cells are clearly of great importance in cancer, being largely responsible for the invasiveness of cancer cells. It is therefore important to note that sarcoma cells, when studied under the same conditions in culture, do not show contact inhibition.

Abercrombie and Ambrose have studied these differences between the social behaviour of normal and cancer cells using the interference microscope which enables the movements at the borders of the cells to be clearly seen. The membranes of isolated fibroblasts are seen to be in continuous undulating movement at their borders. When such an undulating membrane meets the border of another fibroblast, the membranes form an adhesion and the undulations cease. The movement of the cell in the direction of its neighbour then ends. But when a sarcoma cell makes contact with its neighbour, whether it is a normal or tumour cell, the movements of the membrane are not interrupted and no permanent adhesions form. This difference between the behaviour of the membrane in normal and tumour cells appears to be the basis of the lack of contact inhibition in tumours.

Such observations suggest that the alteration in cell–cell interactions in tumours is associated with a change in the chemical nature of the surface. There is evidence to show that calcium ions are involved in intercellular adhesions, because a number of agents which remove calcium are effective in separating the cells of solid tissues. The work of Dr. Coman and his collaborators in the United States on the decreased calcium content of tumours may therefore be of importance in connection with the decreased adhesiveness. Ambrose, James and Lowick have also found that tumour cells carry a higher net negative charge than normal cells, which again suggests that the chemical nature of the cell surface is altered.

So the general behavioural picture of tumours as compared with normal tissue suggests a decrease in the degree of interaction between neighbouring cells. It is interesting to note that Professor J. Z. Young, in his Presidential address to Section D (Zoology) (See *Advancement of Science*, *Vol. XIV*, *Sept.* 1957, *pp.* 48–57) emphasised the importance of studies on the factors involved in interacting groups of cells in normal development. This aspect is of great importance in investigations of interactions between nerve cells, and a mathematical treatment, using information theory which is used in telecommunications, has been successfully applied to the problem. Dr. Goldacre mentioned that a similar approach may be of importance in cancer. Normal development may be associated with a 'brain-like' interaction between tissue cells. A failure of cell contacts may then lead to a disturbance of the interaction pattern and so to the disordered growth of tumour tissue.

Various sensitive physical and biological techniques are therefore being applied to the problem of cell contacts. Dr. Mercer mentioned that the electron microscope now has such high resolving power (down to 10–15 Å) that it is possible to examine the cell membrane directly. The high resolving power combined with the cutting of extremely thin sections has led to interesting results. In normal tissues, it is desirable to choose those in which various stages of development and association can be studied. For example, there is a certain type of social amoeba which leads both a solitary life and a social life in which the cells are aggregated to form a spondilium. Another system in which changes can be observed is the mammalian epidermis, to which we have already referred.

Electron microscopy of these systems indicates that the cell membrane consists of a layer structure about 60Å thick. These layers may correspond to a lipid, lying between two protein layers as suggested by Professor Danielli. In isolated, actively dividing cells the membranes are seen to have a highly convoluted form, but as they make contact with other cells they flatten out, implying that the two surfaces 'wet' each other.

The membranes in contact are generally separated by a distance of 150–200 Å. This separation suggests that a cementing material may be deposited between the cells. In the later stages of differentiation in epidermis and hair this is certainly the case; a series of dense layers can be seen deposited between the cells. There is at the moment little evidence about the chemical nature of the cementing material, but it may be of interest to point out that a group of red blood cells, when agglutinated by an antiserum, also show this distance of about 200 Å, between their membranes. It is therefore possible that a protein molecule, rather similar to an antibody molecule, may be involved in the intercellular adhesions. Tumour tissues, when examined under the electron microscope, often show changes in their cell contacts, as compared with normal tissues. Anaplastic tumours may show a convoluted surface with only small areas of contact, i.e. the surfaces are more like the surfaces of normal cells in the early stages of tissue formation. This result certainly suggests some surface change as in the case of the interference microscopy and the surface charge measurements. It is distinctly possible that the change is due to a loss or decrease in the amount of intercellular cement seen in the electron microscope. So far it has not yet been possible to detect a change in cell contacts in more differentiated tumours which may represent an earlier stage of the transformation.

An extremely sensitive method of studying possible changes in the surface material of the cell was described by Dr. and Mrs. Easty. They have made use of antisera, prepared against tumour cells. The antisera are prepared in a manner rather similar to that used in the preparation of diphtheria, and poliomyelitic antisera, etc. The suspension of tumour cells is carefully washed to remove blood proteins and is then injected periodically into a rabbit. After about 4–6 weeks an antiserum may be obtained and its reaction on various normal and tumour cells examined. Here again, the interference microscope is most useful. When an antiserum reacts on a living cell, the first effect appears to be a reaction with the cell membrane. The early stages may be seen as striking changes of colour in the interference microscope as the cytoplasm flows out through the membrane and the concentration decreases.

Dr. and Mrs. Easty showed a colour film illustrating these effects. When first prepared, the antiserum reacts almost equally as strongly with various normal cells as it does with the tumour cells. There is one exception to this; liver cells are practically unaffected. But if the antiserum is first agitated with a suspension of normal cells, the components which react with normal cells are absorbed. It is then found that the reaction between the antiserum and the tumour cells can be clearly seen as a colour change, but various normal cells, erythrocytes, spleen and kidney cells no longer show any change, but can be seen to be moving actively. These observations indicate that the tumour cells contain structural components similar to those of normal cells. But when these components are eliminated there remain some components which are specific for the tumour cells. These observations were carried out on a tumour which had been transplanted through many generations and the differentiations detected could therefore be due to a difference between the genetic character of the tumour and the host. These experiments are now being followed up by studies on primary tumours, to see if the differences can still be detected in this case.

Dr. Easty also mentioned that it is possible to detect differences between individual cells of the same tumour. When a large number of cells was examined, it

was found that a small proportion (about 10 per cent) were unaffected by antiserum. But when the cells were grown in another strain of mice it was found that about 50 per cent of the cells were resistant to antiserum and were seen in the film to be moving actively after 40 minutes This difference appears to be due to the fact that there is a mixed population of cells present initially, the type which is not affected by antiserum being favoured in the second strain of tumours.

This brings us on to a more important aspect of the biology of cancer, which has been emphasised by Sir Julian Huxley, in some recent reviews. It was, indeed, unfortunate that he was prevented by illness from presenting his paper at Dublin. Huxley considers that tumours should be looked upon as a phylum of obligatory parasites which originate and generally perish with the host. Such tumours are found in both the plant and animal kingdoms. Such parasites will be subject to conditions which provide fruitful studies in adaptation, evolution and population dynamics.

That tumours contain a mixed population of cells has been suggested by a number of observations. For example, Klein and Klein in Sweden have obtained a tumour of differing biological behaviour by selecting and transplanting strains all of which have been derived initially from the same tumour. One way of studying these variations was described at Dublin by Professor Koller. By making cytological preparations under the microscope, it is possible to examine the cells during division when the chromosomes are clearly visible. In normal division, the chromosomes are duplicated and are seen to separate so that an identical set is transmitted to the two daughter cells. But in tumours this is not always the case. As the two sets of chromosomes separate during anaphase, it may be found that one pair of chromosomes is still unseparated, so that the pair produces a bridge between the two daughter cells. This may lead to a disturbance in the number of chromosomes in the daughter cells. Again, division of the nucleus may take place without division of the cell, so that the nucleus acquires double the number of chromosomes originally present (polyploid cells). The divisions in some cases are multipolar. By such processes, the cell population becomes very heterogeneous as the tumour keeps growing by cell division. The normal diploid number of chromosomes is 46, but cells with several hundred chromosomes may be found in tumours. The cancer cell possesses some instability which ensures that variations in the cell population are continuously taking place. It is probable that the change from a hormone-dependent to an antonomous tumour takes place by some such process. Even within the same tumour Professor Koller mentioned that differences are found between the primary and those growing in various metastatic situations. These changes can be understood in terms of the polymorphism of the cells, those which are favourable to a particular site being favoured at the expense of others.

This aspect of cancer is also of therapeutic importance. If a tumour is the subject of early diagnosis, it is likely to consist of a moderately uniform type of cell and respond to a particular treatment. But in the later stages, other cell types are likely to have arisen which are resistant to treatment and continue to proliferate.

We learn from these various accounts that the cancer cell has developed from the normal cell by acquiring certain new characters; firstly, a change from the type corresponding to the tissue of origin to a more primitive type developed by loss of differentiation; secondly, a failure to interact with neighbouring cells and to have its movements controlled, called loss of contact inhibition; this change is associated with a change in the surface properties of the cell; thirdly, a continuous and unstable process of cell division associated with the appearance of new and in many cases more anaplastic types of cell.

The exact chemical and biological mechanism which leads to these changes is much more difficult to investigate. One possibility, mentioned by Dr. Goldacre, is that cancer-producing agents react with the cell membrane. One interesting type

of experiment is to study the effect of cancer-producing agents on the membrane. This is most conveniently carried out on large cells like *Amoeba proteus*, in which the membrane can be clearly seen. In the presence of nitrogen mustard (HN–2) the amoeba puts out pseudopodia which it cannot retract; monofunctional mustards (HN–1) which are much less active biologically are found to have no effect on the amoeba at one hundred times the concentration of HN–2. Diepoxides, which also act as carcinogens, produce a hardening of the amoeba's membrane. Benzene, which produces leukaemia in mice, causes the membrane to be raised away from the cytoplasm. This effect was beautifully illustrated by a film. Dr. Goldacre also produced evidence to suggest that at least a part of protein synthesis takes place at the cell membrane. In the film successive layers could be seen peeling from the membrane and moving back into the cytoplasm, holding back the cytoplasmic granules. These films could represent successive layers of freshly synthesised protein being separated from the membrane. In these terms, the action of a carcinogen would be looked upon as leading to a changed membrane, which leads to altered protein synthesis of layers secreted from the membrane.

But in the last analysis, there is a considerable weight of evidence to suggest that the problem of cancer is a problem of internal cellular transformations leading to altered surface behaviour, mitosis and social behaviour. This aspect was considered by Professor Haddow. At the beginning, he referred briefly to the historical developments which have made such an approach possible. His predecessor, the late Sir Ernest Kennaway, first isolated a chemical substance which can induce cancer in experimental animals. The discovery of the carcinogenicity of dibenzanthracene opened up the possibility of producing cellular changes under controlled conditions. Since that time a very large number of carcinogenic substances have been discovered. Some of these will produce tumours at the point of application, e.g. dibenzanthracene or methyl cholanthrene on the skin. In other cases, the response may be in an organ remote from the point of application, e.g. azo-dyes will induce liver tumours, β-naphthylamine causes bladder cancer, etc. These carcinogenic hydrocarbons are complex chemical substances and their site and mode of action in the cell is little understood. But the experimental approach has been much simplified during the last few years by the discovery of comparatively simple chemical substances which can induce cancer. These are the nitrogen mustards and epoxides already mentioned in connection with Dr. Goldacre's observations on the membrane, also the ethyleneimines. Due to the simplicity of their structure, the ways in which these substances can react with biological molecules are comparatively few. The nitrogen mustards are alkylating agents, the bifunctional types (HN–2) being much more reactive than the monofunctional types (HN–1). Apart from their effects on cell membranes, these compounds produce visible and rapid changes in the structure of the cell. These changes are particularly well seen in the nuclei of dividing cells. Fragmentation of chromosomes, anaphase bridges, interference with chromosome duplication and the production of micronuclei have been studied in particular by Dr. Revell on growing bean roots. Most interesting mutational effects, rather like those seen as the result of X-rays, have been observed in the fruit fly, *Drosophila*. Treatment of the germ cells with these agents leads to the appearance of mutant forms in the offspring. Some of these mutations are restricted to very small loci as has been shown by Dr. and Mrs. Fahmy. These clearly observed effects on the chromosomes suggest that these chemical agents may be interfering with the genetic material of the cell, possibly the nucleic acid. The change from normal to cancer cell would then be due to a similar type of transformation in the nuclear material of a tissue cell.

To understand how such mechanisms can transform the cell behaviour, we need to enter the complicated and highly involved field of cellular biochemistry; we pass out of the field of cell biology. But in general terms, it may be said that the

regulation of normal cells appears to be dependent upon a delicate balance of interacting enzyme systems. Any disturbance of this system is likely to lead to a condition of imbalance, like an unstable electrical circuit. One possible clue to this process was given by Professor Haddow. Administration of xanthopterin to mice causes a wave of mitosis to appear in the kidney tubules. Xanthine oxidase appears to be the enzyme which controls the level of xanthopterin in normal tissues. A reduction in the concentration of xanthine oxidase within the cell would therefore be expected to lead to an increase in the concentration of xanthopterin and so initiate mitosis. Dr. Lewin has obtained some indication that the level of xanthine oxidase is in fact reduced in tumours.

Clearly the biology of cancer covers a broad and interesting field. Some aspects could not even be considered in the limited time allowed at Dublin. Of particular importance is the Rous virus which induces avian tumours. More recently, it has become clear that a number of mammalian tumours, particularly leukaemias, are of viral origin. In this case we are dealing with cytoplasmic particles which are of nucleoprotein nature. When a cell is infected with these particles it is transformed in behaviour from a normal to a cancer cell. Such changes may represent an extreme form of the cellular changes in nucleoprotein already mentioned. However, the evidence does not indicate that all tumours are of viral origin.

Although cancer is an intensely human problem, it presents many attractive and fascinating problems for the experimental biologist. It is possible that a solution to the problem will in fact be eventually achieved by such a detached application of the discipline of fundamental biology.

FOLK CULTURE AND THE PEOPLE[1]

by

G. B. THOMPSON

THE title of this paper is somewhat misleading in suggesting a general treatment of the subject. In fact it is based on ideas formulated for a much more restricted field, namely the creation of an Ulster Folk Museum. This project has been under discussion for some years and has suffered a series of set-backs; but, at the same time, it has grown on paper from the status of a branch of the existing Belfast Municipal Museum to a much larger institution with full provincial standing.

I feel that the delay has been a blessing in disguise for it has given ample time for serious consideration of the ultimate form and function of the institution.

The content of this paper is essentially a contribution to thought on this scheme; but I feel that the views and ideas could be generally applicable.

An institution for the study and preservation of folk-culture material can be of great importance in the social and economic life of the area it represents. It is imperative, therefore, that its creation should be preceded by a clear definition of its purpose and objective lest it is left open to serious criticism in the future. Such a project must be a community effort in which all sections, all groups, all interests, however varied, are encouraged to give their support.

I believe that the Ulster Folk Museum plan is not yet wide enough in conception. By way of expressing the hope that this might be expanded to create a folk institution unique in western Europe, the following opinions are put forward.

WHAT IS FOLK-CULTURE?

Obviously this is a fundamental question which demands a generally accepted definition before anything else can be done. As yet its meaning remains vague. But approach it from what angle you will and it still remains a relatively simple term. A *culture* is a living growth, and *folk* simply means people. So as a subject it embraces the life of people, the interaction of man and his environment, his past, his present and his future.

Certain groups of people exhibit similarities in their way of life, and one can consider them as cultural units. One can talk of west European culture, or of Irish culture, or of smaller units within her shores, according to the detail in which we study them.

In fine detail small cultural units become apparent; in broad consideration these small units merge into larger units. Ireland, for example, belongs to the culture zone of Atlantic Europe. In recent generations we have established cultural connexions with the New World, and our central position between East and West is unique.

But the simple fact remains that the folk-culture of an area is the life of *folk* in that area. It is not the life of the past, nor of any particular period in the past. The life of a community is steady and continuous, changing slowly, and always with a co-existence of old and new in it.

It is both material and non-material in content. It may include an implement, a piece of furniture, a word, a turn of speech or a local flair for drama or music of a particular type. It is a broad, complex subject made up of man's creativeness, ingenuity, practical ability, organisation, enquiry and thought.

No culture is pure, since its changing formula is made up of components from many sources, foreign as well as local. Words like *native* and *traditional* should

[1] A Paper read to Section X, The Assembly of Corresponding Societies, at the Annual Meeting of the British Association in Dublin on September 6, 1957.

be used with care. Very little in any country's culture can be classified as purely *native*. And when, or by what process, does something become *traditional*? A humble spade is virtually universal, only variations of it are *local* or *native* or *traditional*. This applies equally to dialects, folk-music, dancing, the visual arts.

A culture does not lend itself to being departmentalised on a time basis. Some subdivision is necessary for the convenience of detailed study, but it is wrong to impose time restrictions in the initial stages of consideration.

Folk-culture students cannot always assign an accurate date or period to any aspect of the subject. A collection of objects illustrating rural life may include a wooden plough. It might have been used in 1857, but it might also have been used in 1957. The antiquity of it may be interesting, but it is equally interesting that it may co-exist with modern farming machinery as part of technology in the twentieth century. In the same way a word or a phrase may be at the same time modern, medieval, and all periods intermediate.

So in a folk institution our primary task is to study and interpret the life of our chosen area by recording the living past *in* the present, by linking the dead past *with* the present, and by keeping step with our culture as it progresses through the years to come.

Folk Culture Study in the Modern World: Influence and Importance

To appreciate this we must think broadly and futuristically. We must also think universally and not nationally or provincially.

Recent generations have seen developments in a universal move towards standardisation of material and ideological things. Mass production is now such that anything with character and individuality is almost unique. World political thought has resolved itself into a difference of opinion between East and West. Recent trends in connexion with world commerce, more especially with European commerce, show yet another instance of international organisation.

Standardisation on this extreme scale has both advantages and disadvantages. No single political or cultural unit is exempt from the resultant influence. In the extreme these will tend to bring about a weakening, even a destruction, of individual character and creativeness. In this respect standardisation is an evil.

Somehow individuality must be preserved where human culture is concerned, however inevitable standardisation may be in political and economic fields.

In Ireland we do not yet appreciate this sufficiently for our roots are still so much a living part of our daily lives. But in a large unit such as America, where modernisation has reached a relatively advanced stage, and where many people are separated from their native cultures by 3,000 miles of ocean, one sees a different picture. One witnesses a general hunger for tradition in the anxiety to establish ancestral connexions, the love of antique and hand-made objects, the creation of small national units within the bigger single unit, clinging obstinately to more intimate ways. So in a sense the people concerned instinctively seek the best of both worlds.

However advantageous internationalism may be in economic and political spheres man is at his best in a small community. He reacts more faithfully to the loyalty it demands. He is essentially a family man. When this family becomes a nation or a group of nations the *family* analogy is not so apparent to him. Nevertheless, it is significant that in recent years there has been considerable agitation for independence on the part of some countries absorbed in an immense single empire. They have sought to retain some of the major advantages of unity and standardisation by staying within the less restricted limits of a commonwealth, while, at the same time, seeking through independence a more intimate family structure within their own country.

The modern trend towards uniformity must be tempered by the development and preservation of a healthy, balanced, regional awareness. I must emphasise that by this I do not mean a narrow, parochial outlook, nor a passive resistance to progress. The simple fact is that people need a tradition behind them. Call it a form of religion if you wish; it is of the same order. It is a universal need and it must be fed by a deliberate effort to maintain records of past tradition on one hand, and to foster those present-day features of social life which stem from local culture. I emphasise local culture because, as I have indicated, man is more stimulated by things which concern his home surroundings than by those of a broader scene.

In his life-cycle man learns during his progress through the intimate family circle to the broader sphere of school, university, business or industry. In many instances, however, the family and immediate neighbourhood remain dominant influences in that a great number of people continue to live in it rather than move out towards wider horizons. So they tend towards a narrow, restricted viewpoint which directly opposes modern requirements.

Conversely the same narrow viewpoint often gives birth to a form of rebelliousness culminating in emigration. I am not opposed to an adventurous, pioneering spirit, but often the urge to move from home is not so much indicative of this, or of initiative and ambition, but rather of misinformed and misinterpreted ideas about the home region and its society, with an accompanying false sense of values.

Present-day tendencies demand a greater sense of perspective among people than ever before. It cannot suffice that a man be left to attune himself, by himself, to recent advances in technology and ideology. The recent rate of advance, like progress at any time, has been such that many people have been left far behind in a system which to them is modern, but which is, in fact, outmoded.

What is needed is something which, in spite of standardisation, will maintain family or cultural solidarity, and emphasise its proper place in the scheme of things. Man must be able to see himself and his own heritage against the broader pattern of others and their heritage. In this way he will see both differences and similarities, and thus develop a balanced attitude to his own society and to others.

I believe that this is wherein lies the essential justification for a folk institution, although in saying this I am not being indirectly critical of those who study folk-culture for love of the subject. On the contrary, their efforts, whether on an amateur or professional basis, are vital and to be encouraged. I submit, however, that someone must accept the added responsibility of ensuring that the resultant information does not remain a mere static record. There is an obligation to the public, especially when the work involves expenditure of public funds; and a project to establish a folk museum indicates an acceptance of the challenge which this obligation presents.

Folk Museums: the Popular Conception

Up to date I have avoided, where possible, reference to a folk *museum*. Institutions established under this heading must, by the very meaning of the term, concern themselves almost entirely with *bygones*. Those folk museums which already exist and which have grown from the Scandinavian prototype at Skansen in Stockholm have one thing in common—they preserve the past. Indeed in most instances so comprehensive a description is an exaggeration. It would be more correct to say that they preserve certain aspects of the past.

Each one has its limitations resulting from a variety of factors, which include, for example:

1. *The availability of material*
   Working only with the past one is inevitably too late on many occasions with the collection of material. Collections inevitably have serious gaps in them.
2. *The limiting factor of available finance.*

3. *The personal interests of the curatorial staff*
   These are sometimes reflected in an unbalanced collection, although this is something which cannot be too severely criticised; the shortage of individuals sufficiently trained in the requisite variety of subjects which make up folk-culture is universal. Nor would it be possible to employ them all if they were available.
4. *The varying interpretations of folk-culture*
   Some museums concentrate on rural life, some on urban life, some on certain aspects or periods of either of these, some on selected levels of society.

Nor can this be criticised too severely since it is closely related to the availability of material, and to the fact that by concentrating on material things one cannot ever hope to achieve an adequate coverage of social life in any form.

Yet folk museums are being created, or at least advocated, in several countries, all based on the popular conception of an open-air exhibition of re-created buildings with, perhaps, a supplementary, centralised, indoor collection of small objects. And as such they do excellent work—within their limitations. But all too often—and this may well be applied to most museums, folk or otherwise—they cater for, and attract, only that person who is already knowledgeable and interested, and who, if he did not find interest and stimulus in a museum, would find it elsewhere.

In many instances existing folk museums could be described, perhaps, as having been born of a human urge to collect, to reminisce, to study history in one form or another. Yet the factors determining which material shall be studied and collected have all been temporal; after all the extent to which a bygone is a bygone can only be measured against its most recent counterpart.

In present-day folk museums the collections consist of objects whose interest and significance are largely relative to the time at which they were collected. The same significance will not necessarily hold for visitors fifty years hence. A folk museum established in 1957, and composed of exhibits which have been selected according to 1957 standards and the 1957 viewpoint, is just as liable to become overgrown with moss in 1987 as it is to increase in appeal by the difference in 1987 standards and viewpoint.

Recently a schoolchild, answering a questionnaire issued by the Committee on Ulster Folk-life and Traditions, wrote in reply that '*in olden times* the people of Belfast used to ride about in tramcars'. Trams were replaced by buses in Belfast a mere five years ago!

In summary, then, a folk museum often is, today, a collection of material representing the life of an age which is past, and exhibited, where possible, in open-air, naturalistic surroundings.

This is approximately the pattern by which most existing museums of this type have been established, and within which broad framework they assume their varied forms.

Folk Centres: An Alternative Suggestion

Criticism of the existing policy, and of the resultant institutions, demands justification in the form of an alternative. Obviously this will be governed by the broader definition of *folk-culture* already suggested. It will be readily appreciated that by accepting it more or less unconditionally as the *life of people* it will embrace considerably more than the preservation of the past. So our folk institution will be devised in a manner which enables it to move step-by-step with modern society, and to cover all aspects of it. It will therefore be flexible and capable of expansion by virtue of an unhibited policy.

The living character of a community at a given time is expressed through the hundred-and-one pursuits which make up the daily life of people. This is both

human and timeless. The life—the culture—of today is the folk tradition of tomorrow. Why wait until it has become an incomplete series of survivals before studying its significance and virtues?

If folk-culture study, especially the study of the past, has any merit, or has anything to teach us, it must be capable of becoming *applied* folk-culture study, and this can only be achieved by applying it to the life, more particularly the young life, of the present day.

Yet this is precisely what people, by their very nature, unconsciously do for themselves. They bring their own experience and knowledge acquired from their forebears into the pattern of their daily lives and those of their offspring. So it remains, therefore, for this process to be highlighted and made obvious.

I suggest that the most practical and effective way of doing this is to create a system which promotes a greater degree of collaboration between related activities of modern society—something which would emphasise the interdependence of human activities, whether individual or group, voluntary or statutory. Such a plan would at one time analyse and synthesise a given society, and at the same time effect a closer relationship between them.

The term *folk museum* is being avoided since it is immediately and completely suggestive of the past. As a substitute the term *folk centre* is adopted, which, though recognising the importance of preserving the past, does not advocate it as its primary aim, but rather suggests it as an essential part of a bigger organisation.

The folk centre, in short, could become a type of parent body through which individuals and groups might achieve a greater degree of proximity with those pursuing interests parallel or complementary to their own, and from which material assistance and benefit will result.

An Ulster Folk Centre

In Ulster we have numerous organisations, statutory and non-statutory, each one responsible for one or more aspects of Ulster development. These consist, for example, of museums governed by borough, county or municipal administration; the university; colleges; schools; field clubs and societies in the form of voluntary adult bodies or as extra-mural additions to school and college curricula; organisations covering music, drama and the visual arts, social service, adult education, industrial development, archaeological and historical research and the study and collection of folk-life material.

Each one of these is part of a great complex pattern of human activity in the Province. Each one adds something to, takes something from, learns about, teaches about, studies, moulds, and, in general, exists as an offspring of this pattern. But as conditions exist at present no single unit in the pattern looks for any great distance beyond its own boundaries to see the complete picture, or to appreciate as fully as possible the interdependence of each unit. Of course, there is not, as yet, any central co-ordinating core to which they can turn for this purpose, or which can promote this end.

I have already stated that the proposed folk museum should be but a *part* of this bigger scheme; furthermore, it would be the essential part, for it would constitute a *book of reference*—a physical nucleus—from which other services could develop and radiate. It would also remain as a visible symbol of the principles under which the folk centre operates.

Its collections in storage, in exhibition halls, and in an open-air park, would be supplemented by documentary and pictorial material. There should also be a detailed index of such relevant material as is housed in other institutions.

However, there is the difficulty that under the suggested broader definition of folk-culture the collections of physical objects would become expansive beyond control. The solution to this is not to impose an unjustified time limitation as a

necessary qualification—we cannot start folk-culture at 1650 and stop it at 1900—but rather to collect more systematically and to resist the impulse to hoard *anything* merely because it is antiquated or unique. An organised sub-division of material culture would guide the selective collection of *type* specimens. Others which are essentially duplicates or minor variations would require only documented preservation.

It must always be borne in mind that material culture, like other aspects of life, is constantly changing. The invention of today is the period-piece of tomorrow. In our collections we must leave ample room for expansion.

Now having created the reservoir what can it supply? It cannot remain static but must flow.

We have suggested earlier that it should first use its unique character to establish closer and more effective collaboration between related bodies. I regard this as a principal objective, for it would create the outlet for the rest of its potential uses.

This might be achieved in Ulster by the creation of an Ulster Society or Ulster Association based in the folk-centre and essentially administrated by a voluntary council of leading figures in various walks of life. This society could have a system of institutional and individual membership.

I do not propose to go into details at this point except to add that the manner in which societies ally themselves with the British Association in Section X seems a fitting comparison. In Ulster a similar type of relationship exists within the sphere of agriculture through local farming clubs and the Royal Ulster Agricultural Society.

One development which could emerge from this would be the creation of local county committees, which would be a more effective means of distributing responsibility and benefit evenly throughout the Province than a recent suggestion of branch folk museums. I even envisage these as possibly becoming, in a sense, complementary to existing statutory county councils whose duties are clearly defined and limited.

There might be an annual Ulster Society meeting, conference or exhibition held in a different provincial centre each year and organised, perhaps, on lines similar to the British Association. This would be one period when the whole provincial jig-saw would be knit together and viewed in its entirety, in the same way as the fabric of science is unrolled this week.

Consider another aspect. For some time now in Ulster there have been suggestions of a school of local studies at university level. Up to date this has not materialised. Here too is a possible outlet for folk centre potential. In the same vein there has been a tendency in some Ulster schools to introduce local studies as part of the curriculum. Regrettably this is in danger of being discontinued for lack of organised support at administrative level, and for lack of a central information bureau from which the inspiration and knowledge could come. Therefore local education at all levels has not yet been successful in creating an effective and beneficial course in the subject. A folk centre could well be of considerable value in co-operating with education authorities to remedy this discrepancy.

At the moment I am completing a survey of rural industries for the Northern Ireland Council of Social Service, on which will be based a project aimed at increasing rural prosperity and employment opportunities through small, and essentially craft, industries. A local rural industries bureau, if such develops, will tackle problems such as marketing, instruction and design. Here, too, a folk centre could play a vital part in becoming a shop window for the products of Ulster crafts, or in providing information relating to traditional designs and techniques, or again in maintaining selected crafts as functional exhibits.

Tourism is a vital industry in Ulster. One cannot fail to see immediately that an active folk centre, with its museum attached, would be of the utmost benefit to

the tourist and the industry alike. Not only would interest in more distant parts of the Province be stimulated, but the visitor would acquire a ready appreciation of the difference between authentic and bogus, as well as differences in regional character. Furthermore, local districts through their county committees could possibly do much in co-operation with the folk centre and the Northern Ireland Tourist Board to improve facilities in their area.

The greater degree of cohesion which a folk centre could create between present somewhat scattered elements of local drama, music, art and literature would solve many of the existing problems in these separate spheres.

These are but a few of the possible outlets for a vigorous unit, by which it would become a living part of the society which created it. As such it would meet people halfway—meet them in the familiar, understood surroundings of their individual and group interests. In addition it would not be too conservative to sell itself through the modern communicating media of film, television and radio. In short it would keep pace with society's progress and would become, in effect, a measure of past experience against which a society could calibrate its sense of values so essential to sound future planning. Through it we could show ourselves to ourselves, and we could present ourselves in true perspective to the outside world.

If we could dare to visualise parallel developments elsewhere, based on an agreed concept, we would find little difficulty in directing a permanent spotlight on the important cultural differences throughout the world, and, in particular, the essential cultural similarities.

It is especially urgent that young people should be equipped with a sound knowledge of their heritage, particularly those who, by some agreed process, could be recognised as potential leaders of the community. Thus I would lay great stress on the co-operation between the folk centre, the education authorities and the schools. Furthermore, assuming for the moment that similar institutions existed elsewhere, I would like to imagine them developing greater facilities for enabling young people to travel and study abroad, to experience the stimulus of getting to know their counterparts in other countries, and to have the chance of viewing their own culture in the light of a new environment.

In summary, then, our aim should be to give form to the spirit of our country and through it to acquire a deeper insight into what Dr. Estyn Evans described as 'the spiritual fabric which clothes the material world'. I suggest that this is true folk-culture, and by this we are not defining *folk* as a decadent minority of quaint beings with old-world ways. You and I are *folk*. It is our culture and that of our kinsmen we hope to study and understand, and then apply to the enrichment of our daily lives.

I think we could be on the threshold of something as yet unique in the social fabric of any country. Lying as we are between the eastern and western worlds it would be fitting if we were to set the pattern of effort necessary for this work.

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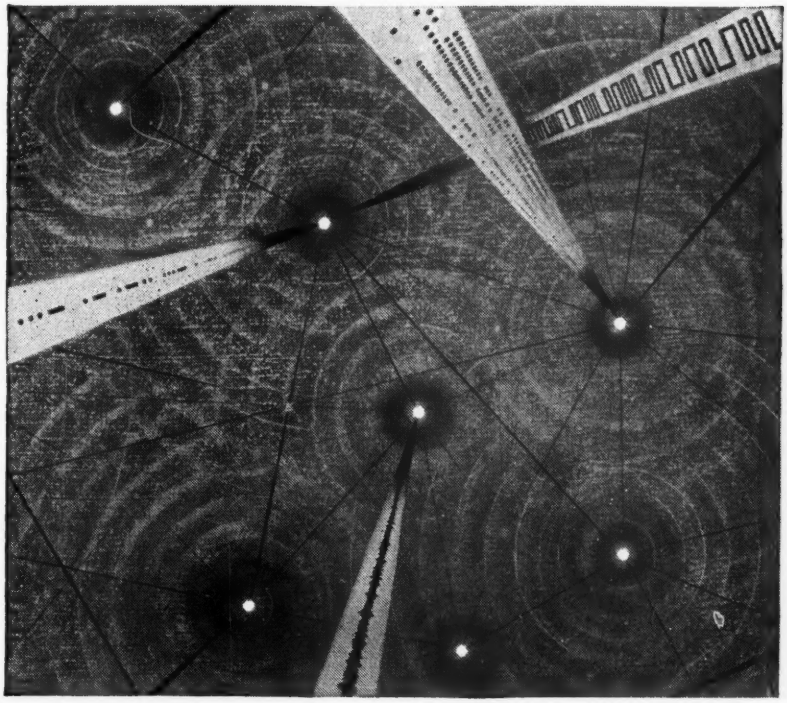

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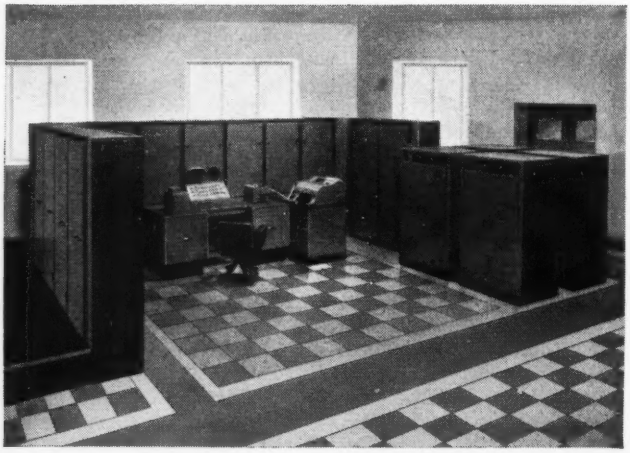

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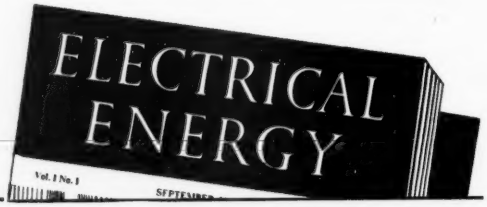

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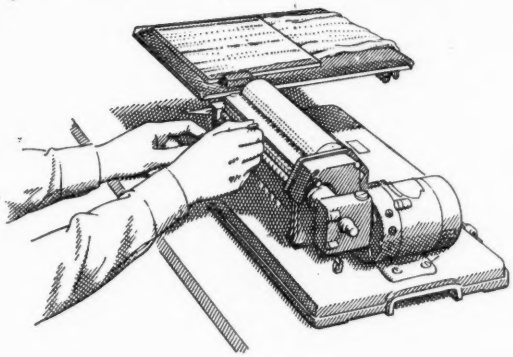

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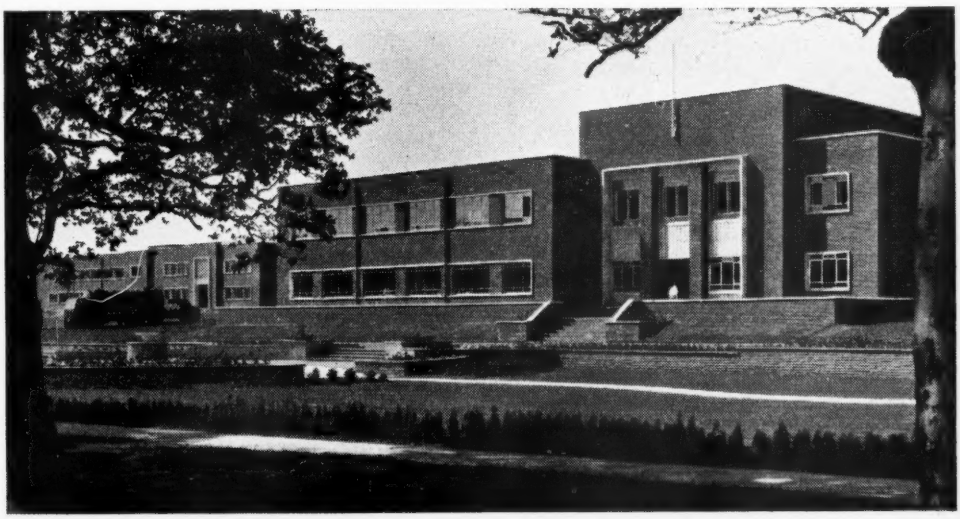

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